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1908-09

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THE
NEW PHYTOLOGIST,

A BRITISH BOTANICAL JOURNAL.

EDITED BY A. G. TANSLEY, M.A., F.L.S.,

UNIVERSITY LECTURER IN BOTANY, CAMBRIDGE.

VOLUME VII.

PP. VIII. AND 262.

WITH FIVE PLATES AND 40 FIGURES IN THE TEXT.

CAMBRIDGE, 1908.

PUBLISHED BY THE EDITOR AT THE BOTANY SCHOOL.

Charles II

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1908-09

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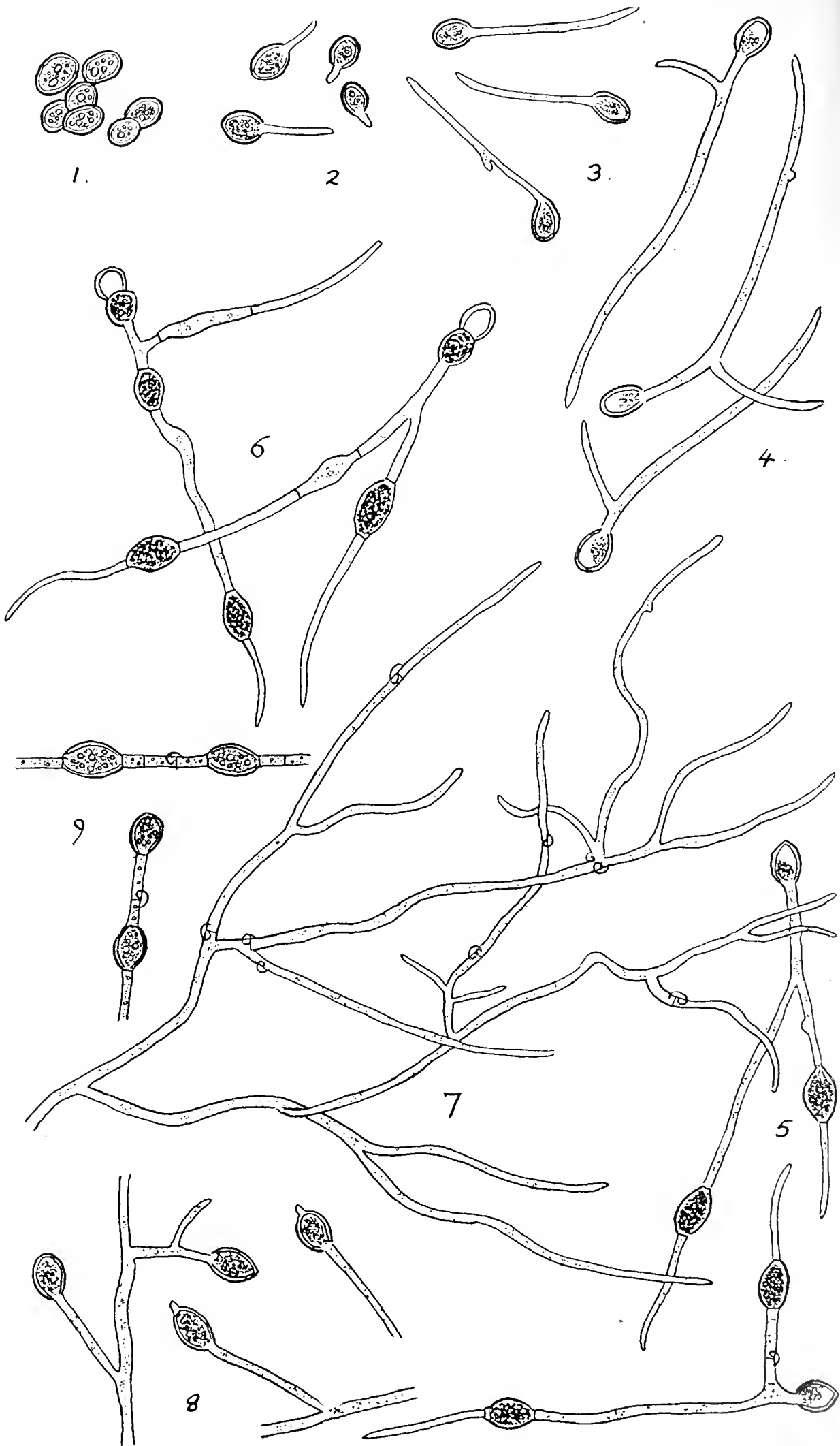
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D. Marryat del.

MARRYAT—CHLAMYDOSPORES OF *PLEUROTUS*.

T H E

NEW PHYTOLOGIST.

VOL. VII., No. 1.

JAN. 31ST, 1908.

LECTURES ON THE EVOLUTION OF THE FILICINEAN VASCULAR SYSTEM.¹

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LECTURE IX.

THE LEAF-TRACE. ONTOGENY.

[FIGS. 96—101].

A GENERAL VIEW OF THE FILICINEAN LEAF-TRACE.

THE leaf-trace and petiolar vascular system of Ferns, though correlated in a general way with the structure of the stem-stele, has a semi-independent course of evolution, which it is necessary to consider separately.

It is mainly to Bertrand and Cornaille², and to Gwynne-Vaughan that we owe anything like a comparative treatment of this subject during the last ten years, a period which has seen for the first time a deliberate treatment, particularly in this country, of the problems of Filicinean vascular anatomy from the evolutionary point of view.

The French authors have accumulated a great quantity of interesting data, but the method of comparison they employ is based on a system of morphological units which seems to have but a limited value, at any rate from a phylogenetic standpoint. Gwynne-Vaughan has done good service in calling attention to the fact that the arched type of leaf-trace or some clearly derived form, is found in the vast majority of Ferns and is certainly to be regarded

¹ A Course of Advanced Lectures in Botany given for the University of London at University College in the Lent Term, 1907.

² See especially, *Étude sur quelques caractéristiques de la structure des Filicinées actuelles*, I. Lille, 1902.

as typical. A brief sketch of the subject from the point of view of these lectures must be attempted here.

At the beginning of the course we saw reason to believe that the primitive Filicinean leaf was a specialised branch of a primitive thallus, a branch originally of the same morphological nature as the axis from which it arose. On such a hypothesis, the vascular strand of the branch would be primitively of the same nature as that of the main axis. Though modifications of the vascular system of the upper part of the foliar branch might be expected to occur at once in relation to the distribution of the assimilating surface, the insertion of the foliar vascular system upon that of the cauline axis ought to show signs of its original nature. As was shown in the second and third lectures, we do actually find, in the Botryopterideæ and Hymenophyllaceæ, the base of the leaf-trace exhibiting a structure which may be interpreted in this way. In the former family we find that it is nearly or quite iso-diametric, though its diameter is very much less than that of the stele, a mechanical necessity where the axis bears crowded leaves. In the Hymenophyllaceæ the base of the leaf-trace (at least in many cases) is identical in structure with that of the cauline stele. The structure of the petiolar vascular system itself is very varied in the case of the Botryopterideæ, whose members bore complex and varied fronds. In the Hymenophyllaceæ, where the demands for water-conduction are much less, owing to the prevalent hygrophytic nature of the frond, the petiolar strand remains much simpler, and in certain types, which we may regard on other grounds as relatively primitive, it very largely retains stem-structure.

The relations of the peculiar petiolar strands of Botryopterideæ were sufficiently dealt with in the second lecture, so far as the data at present available permit.

When we come to consider the series of modern Leptosporangiate Ferns, certain broad facts are at once obvious. As we pass from the protostelic to the solenostelic forms we find the leaf-trace taking on a corresponding expansion. Boodle has attributed the origin of the solenostele, with its increased diameter, to the necessity for accommodating the insertion of broader leaf-traces, thus implicitly recognising the fact, which seems to be indisputable, that the leaf-trace leads, and the stele follows, in the course of evolution. Let us consider, a little more in detail, the probable course of events. The increased diameter of the leaf-trace will necessarily tend, it would appear, to lead to a failure to develop

vascular tissue in the middle of the adaxial (upper) side. The current of water entering an expanded leaf-trace will tend to be diverted to the parts continuous with the periphery of the stele below. This will lead to a failure to develop tracheids in the acroscopic angle between stele and leaf-trace, or, as we may call it, the "axil" of the trace. Thus the leaf-trace will acquire a kidney-shaped cross-section and the same tendency, if carried further, will lead to the formation of the arched type, which sometimes co-exists with a proto-stele (*Gleichenia flabellata*, Fig. 40A). This in turn will necessitate a further increase in the diameter of the stele, and will lead to the formation of a passive tissue (or pith) in its centre, since if the stele remained solid the central mass of xylem would increase in amount much faster than would be required. This pith will naturally tend to be a basipetal continuation of the passive tissue in the concavity of the arched leaf-trace. Thus we arrive at the typical solenostele with its typical arched leaf-trace, the departure of which causes a gap in the vascular wall of the stele.¹ When the leaves are remote and the leaf-trace approximates in size to the stele itself, a section taken immediately in front of the point of insertion will show two similar arcs of vascular tissue with their concavities facing one another, closely resembling the appearance of a section taken just in front of the dichotomy of the stele below a fork of the stem (e.g., in *Gleichenia pectinata*). Thus the adaxial gap in the leaf-trace is fundamentally a result of the failure to develop xylem in the "axil" or region left between the two diverging currents of water, accentuated by the broadening of the leaf-trace itself and the corresponding broadening of the stele, while the gap in the stele and the formation of pith is due to the same cause, whose effect is carried down into the internode below as the starvation of water is felt by the central portion of the widening stele. The stelar gap has to be repaired sooner or later, above the departure of the trace, because of the insertion of the leaf-traces above. To put the matter more strictly, the failure to develop vascular tissue in front of the insertion of the leaf-trace does not extend forward along the stele indefinitely. The currents of water passing into the next leaf-trace situated in the neighbourhood of the same longitudinal line will necessitate the development of vascular tissue in front of the gap. The adaxial gap in the leaf-trace itself

¹ The origin of the *Lindsaya*-type, which involves the formation of internal phloem and typically precedes the formation of the solenostele, is here omitted for the sake of simplicity. It has been fully dealt with in the fourth and fifth lectures.

is, however, in a different position. The function of the petiolar vascular system is to supply the branches of the frond (pinnæ) which come off right and left in one plane. This function is performed mainly by the sides of the leaf-trace curve, while the dorsal or central part of the curve runs on up the rachis, gradually diminishing in size as its lateral tracheæ are drawn into the supply of successive pinnæ. Meanwhile the gap on the ventral (upper) side of the petiolar strand is not closed, because there is no reason why it should be, since there is no demand for conducting tissue in that region. In a good many cases on the other hand, the petiolar system is entirely concentrated in the two lateral strands which directly supply the pinnæ, the leaf-trace splitting into two shortly after leaving the stele (Fig. 55A), or even, in many of the more advanced types, leaving the stele as two separate lateral strands, so that the dorsal (abaxial) strand is not developed at all (Fig. 53A).

The complications of the "horse-shoe type" of petiolar system, are, as we should expect, mainly elaborations of the lateral parts of the primitive strand. These elaborations fall under two heads. First is *the incurving of the free ends of the leaf-trace arch*, which begins in quite simple types (e.g., *Gleichenia*, Figs. 38A, 41A). In the extreme case the free ends become as it were spirally wound on each side within the general contour of the primitive curve. *Matonia pectinata* (Fig. 61Y) shows a highly developed case of this elaboration, but it is also well developed in many Cyatheaceæ. Secondly we have the formation of *lateral folds*, i.e., of a bay in the centre of each side of the primitive curve. This modification, but slightly developed in the *Hypolepis*-type (Fig. 66, 1c), in which the bays are quite shallow, but in *Pteris incisa* var. *integrifolia* (Fig. 65), and in *Pteris aquilina* (Fig. 76) the lateral folds are very deep. In many Cyatheaceæ the two types of elaboration co-exist (Figs. 69, 97).

It has been shown in previous lectures that both of these types of elaboration commonly occur in connexion with an internal cauline vascular system, which in some cases at least appears to be largely, though not primitively, a basipetal development into the stem of the complications of the petiolar system.

It seems, though it is a point difficult to prove on the data at present available, that the elaborations of the petiolar system must have been developed in relation to an increase in the assimilating surface, either in the size or the number of the pinnæ, or in both. This view is quite in accordance with the size of the fronds in the

Ferns whose petioles exhibit highly developed complications of the sort. The very large fronds of such forms as some species of *Gleichenia* and *Lygodium* at first sight seem to contradict this conclusion, but it must be remembered that these fronds with their dichotomous branching have the assimilating laminæ scattered over a much greater length of rachis in proportion than the comparatively concentrated fronds of such plants as *Matonia* and the Cyatheaceæ. It is the crowded insertion of numerous large pinnæ that demands a great increase of the vascular supply-channels of the petiole, and in the sympodial branches of the frond of *Matonia pectinata*, on which the successive pinnæ are very closely crowded, the continuations upward of the incurved free ends of the petiolar strand are actually detached as separate internal systems which contribute to the successive pinna-traces (Fig. 96).



Fig. 96. *Matonia pectinata*. Diagrams of successive transverse sections through upper part of young frond, showing the breaking up of the petiolar strand, and the successive formation of pinna-traces from the sympodial strands on each side. It will be seen that the peripheral pinna-traces are derived from the ventro-lateral angles, and from the incurved free ends of the petiolar strand (the latter being detached and enclosed within the sympodial cylinders as accessory internal systems), both of which parts represent the latest complications of the petiolar system. From Seward.

The petiolar system of the Cyatheaceæ is very characteristically broken into a number of kidney-shaped strands—"divergents" as they are called by Bertrand and Cornaille—each with one protoxylem (Fig. 69). In the less highly developed forms this breaking is incomplete, though the outline of the curve is waved, the waves corresponding with the successive divergents. The continuity of the curve is also commonly broken at the bottom of each lateral fold, the ventral (upper) limb of each fold sometimes becoming continuous with the corresponding limb on the opposite side so that the petiolar system is separated into two curves, both facing towards the ventral (upper) surface. Each pinna-trace is inserted on both limbs of the

fold, the lower or dorsal arc of the pinna-trace being derived from the dorsal margin and the upper or ventral part (*i.e.*, the two ventral arcs), together with the ventral limbs of the lateral loops, arising from the ventral (upper) margin of the lateral fold of the petiolar system (Fig. 97). The vascular system of the pinna has

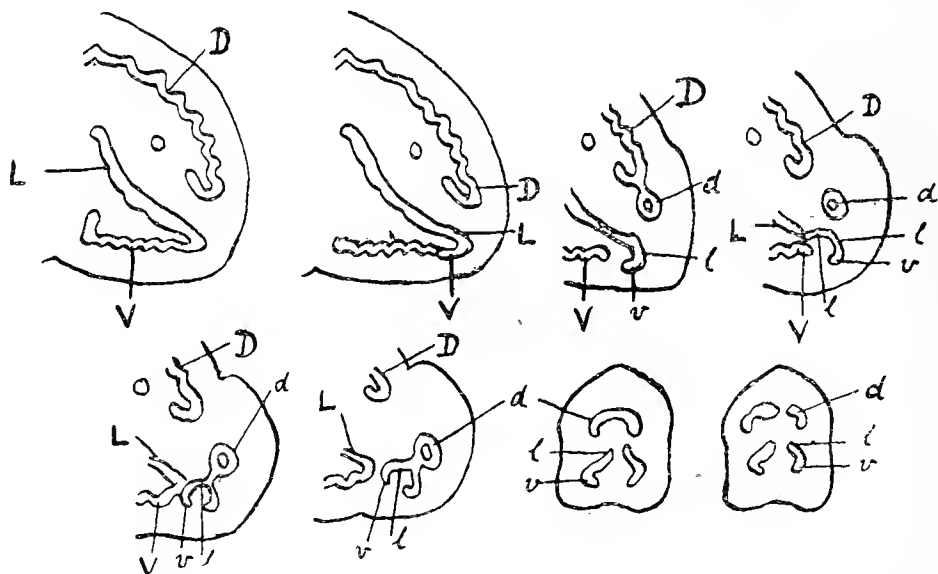


Fig. 97. *Cyathea excelsa*. Diagrams showing insertion of trace of secondary pinna on vascular system of primary pinna. The last two diagrams represent transverse sections of the base of the secondary pinna. *D*, *V*, *L*, dorsal and ventral arc and ventral limb of lateral loop of primary pinna system; *d*, *v*, *l*, ditto of secondary pinna system. It will be seen that the latter departs from the two edges of the gap bordering on *L*, and that each part arises from the corresponding part of the parent axis.

the same general form as that of the petiole, though it is of course on a smaller scale. It is difficult to resist the conclusion that the lateral folds of the petiolar system have been elaborated in relation to the insertion of numerous large pinnæ. It will be seen that they are developments of the edge of a gap bearing very much the same relation to the pinna-trace as the leaf-gap in the cauline stele does to the leaf-trace, and when we remember that the elaboration of the internal accessory system of the stem is connected in these forms with the elaboration of the leaf-trace, the analogy becomes very fairly complete. Thus we seem able to extend the "basipetal evolution" of the vascular system, which as we have clearly seen, obtains in the evolution of the cauline stele, back into the frond, and to base it upon the increase in size and complication of the laminal system. It must of course be remembered that the evolution of the vascular system in the frond still has to be worked out in detail. The available facts are much too scanty to permit us to do more than suggest the main lines upon which this evolution has proceeded.

In the Marattiaceæ the internal accessory strands of the

petiolar vascular system have clearly arisen, as Gwynne-Vaughan has shown, in a different way from the internal strands of the petiole in the Leptosporangiate Ferns. They do not form elaborations of the main petiolar curve, but arise individually from the dorsal (lower) strands of the curve. They are, however, connected (see Vol. VI., p. 230 and Fig. 72E), through the ventral strands of the curve, with the pinna-traces, and no doubt fulfil the same function, in part at any rate, as the lateral folds of the Cyatheaceæ.

The breaking of the leaf-trace into separate strands, which is found in all the higher dictyostelic ferns and in the Marattiaceæ, is probably somewhat the same phenomenon as the "perforation" of the cauline stele (p. 192) with which it often co-exists. In a certain sense it is to be regarded as a reduction-effect, since it is clear that less conducting tissue is produced than would be the case if the petiolar curve or stelar cylinder formed a continuous plate of vascular tissue. The tendency is to the formation of a separate vascular strand (a divergent) in connexion with each protoxylem,—or sometimes a bi-polar bundle between two protoxylems—leaving spaces of ground-tissue between. This would seem to be the result of some factor, such as an increase in the circumference of the entire system, leading to the disappearance of such parts of it as are no longer required for conduction. Here again the petiolar system is often in advance of the cauline stele, for we often have a "broken" leaf-trace associated with a non-perforate stele, but not the reverse case. Of the factors which actually determine the lines of flow of the water current and hence the formation of the isolated strands, we are, however, ignorant. An investigation of a few simple cases from this point of view would be a useful piece of work.

THE ONTOGENY OF THE FILICINEAN VASCULAR SYSTEM.

The characteristic difference between the construction of the typical animal body and that of the typical plant is the compactness of the one and the elongated branched form of the other. This depends directly upon the distributed growth, limited in time, of the animal as contrasted with the localised but continuous growth at the apices of the axes in the plant. The fertilised egg gives rise to a miniature plant which in the higher forms at least grows almost entirely by means of localised *meristems* as they are called, *primary meristems* situated at the ends of the axes, and in some cases *secondary meristems* arising within the axes. Confining our attention

to the first, which bring about growth in length, we find that as this progresses the apical meristem gives rise to a structure of gradually increasing elaboration, till the highest complexity of primary structure attained by the species is reached.

Thus while the whole ontogeny of the typical animal is a gradual metamorphosis of the egg into an embryo, and of the embryo into an adult organism, the greater part of the ontogeny of a vascular plant is a process of addition in space, a building up bit by bit of an increasingly complex structure upon the original simple structure. In this way there is retained a record of the ontogenetic development in the first formed parts of the axis, a record which in the animal body is largely lost as development progresses.

The comparatively complex structure eventually attained by shoot-axes of vascular plants which reach any considerable size, cannot of course be adequately supplied with water and dissolved mineral food from the soil through the slender channel furnished by the first formed primary axis. Either the primary root must branch and form new absorptive organs, itself increasing in size and complexity by secondary thickening so as to form a sufficient conducting channel between the newly formed absorptive organs (its branches) and the shoot-axis, or new roots must be continually produced on the shoot-axis itself, so that the more complex parts of the shoot-axis with its branches are directly supplied from the soil and are not dependent on the first formed parts of the plant at all.

The former method has been adopted by the typically dominant modern plants, the dicotyledonous and coniferous trees; and we have palæontological evidence that it was adopted also very largely by the dominant arboreal Palæozoic and Mesozoic plants. This method is clearly the condition essential to the successful establishment of the erect arboreal habit in which the shoot-axis rises a considerable distance above the surface of the soil.

The latter method on the other hand is characteristic of the great group of Ferns, with which these lectures are concerned, as well as of nearly all the other existing Pteridophytes, and of many herbaceous Angiosperms as well. The erect habit, and a considerable stature, have, it is true, been attained by certain plants, both Ferns and Monocotyledons, which have no secondary thickening. Without entering into the different methods by which the Tree-ferns and the Palms have been able to establish the arboreal habit, it may fairly be said that they are of the nature of short cuts to success, and

the plants which have practised such methods, though successful in a degree, have not become dominant and replenished the earth.

The vast majority of Ferns have either a creeping rhizome, subterranean or superficial, or a short erect stem ("rootstock"), for the most part buried in the soil. Nearly all the members of the more primitive families of modern Ferns, such as Hymenophyllaceæ, Gleicheniaceæ, as well as others with a more advanced type of soral structure, but a relatively primitive vascular system (Dennstædtineæ, Lindsayeæ) are characterised by a creeping rhizome, often with long internodes. It might, perhaps, be thought that the protostelic and solenostelic vascular system is an adaptation to the creeping rhizome, but this notion is negated by the fact that the creeping stems found in many Davalliaceæ and Polypodiaceæ are dictyostelic. Also Lachmann ('89) has shown that the creeping rhizomes of the primitive types have roots either distributed all over the surface of the stem or confined to the lower side, but not localised in relation to the leaves. Such a distribution we should expect in primitive forms. It is in the higher dictyostelic types that the roots are sometimes localised in relation to the leaf-insertions, clearly a more specialised arrangement. In all cases, however, fresh roots are formed close to the apex as growth in length proceeds and fresh leaves are developed, and in all cases there is a tendency, frequently very marked indeed, for the earlier formed parts of the stem to die off as the new assimilative and absorptive organs are developed from the apex.

Owing to the fact that the fern-plant has a continuous uninterrupted development from the egg, and no secondary thickening, the successive stages in the development of their adult shoots can frequently be traced very fully. The earlier ontogenetic stages, instead of being obliterated by the later ones, as in animals and to some extent in the flowering plants, remain recorded in the first formed portions of the shoot, and are only obliterated by its gradual decay. In accordance with the law of recapitulation we should expect this ontogenetic record to represent, in a general way, the history of the evolution of the race, and as a matter of fact these anticipations are strikingly realised by the close correspondence of the developmental evidence with that derived from a comparison of the adult structure of the different families.

Let us confine our attention at first to the monocyclic forms. We always find a protostelic structure in the first formed stem, and in the protostelic types, so far as evidence is available, this structure

is retained throughout the stem, the stele merely increasing in size in relation to the larger and larger leaf-traces that have to be supplied.

Of the ontogenetic history of the *Lindsaya*-type of stele we know, unfortunately, nothing; but when we pass to the solenostelic type we find that the first formed stele is again a protostele, giving off simple leaf-traces, that it then passes through a *Lindsaya*-phase, in which an internal phloem, continuous with the inner phloem of the leaf-trace appears in the centre of the stele. This internal phloem may, in the first instance, form a series of "pockets" ending blindly below, one in connexion with each trace (Fig. 98).

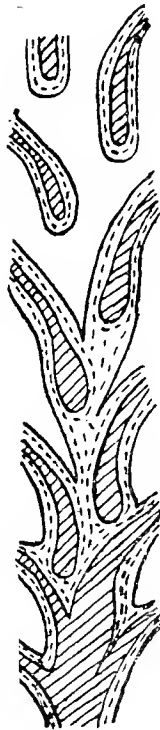


Fig. 98. *Alsophila excelsa*. Diagrammatic median longitudinal section through stele of young plant showing breaking up of protostele by phloem and ground-tissue pockets. After Gwynne-Vaughan.

These pockets, at first independent, soon join as we pass up the stem, to form the continuous core of phloem characteristic of the *Lindsaya*-type. Then an internal endodermis, continuous with the outer endodermis at the "axil" of the trace and enclosing a pocket of ground-tissue continuous with the cortex, appears, extending downwards into the stele from in front of the point of insertion of each trace. A continuous pith is eventually formed by the coalescence of these pockets, and the typical solenostelic condition is thus arrived at.

In the dictyostelic forms the early history is the same; the

Lindsaya-stage and the solenostelic condition are passed through, but the crowding or the elongation of the leaf-gaps eventually leads to their overlapping, and thus to the apparent breaking up of the solenostelic cylinder into separate strands (Figs. 98, 99, 100). Sometimes one or other stage is omitted, *e.g.*, the solenostelic condition in Fig. 100, or the stele passes straight from the protostelic to the dictyostelic condition (Fig. 101), somewhat as in *Marattiaceæ*. In the "perforated" types, gaps other than leaf-gaps begin to arise as the dictyostele increases in diameter.

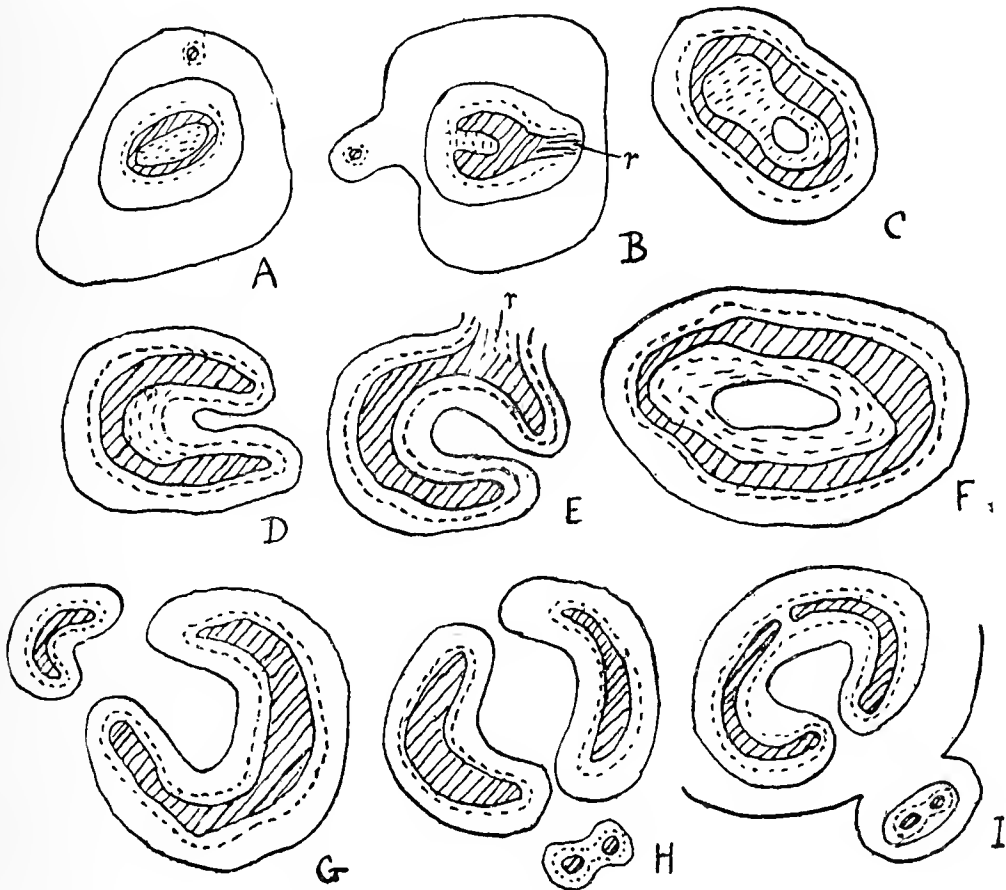


Fig. 99. *Nothochlana sinuata*. Ontogenetic evolution of dictyostely through solenostely from the *Lindsaya*-type (amphiphloic protostely) by the development of ground-tissue pockets which are from the first in connexion to form a pith (C—F) within the internal phloem, and the subsequent overlapping of successive leaf-gaps. A, Amphiphloic protostely. F, Solenostely. H, Dictyostely. From Chandler.

The only polycyclic form whose development has been worked out in adequate detail is *Matonia pectinata*, and here we find a complete series of stages, from the protostelic condition in the very young plant to the tricyclic solenostelic type in the largest rhizomes. The later stages of this ontogenetic evolution we have already traced, in the sixth lecture.

With regard to the earlier, the stele passes through a definite *Lindsaya*-phase, and then through a phase with internal endodermis alone, before a pith appears and the solenostelic condition is reached (Fig. 60, B, G, J). The phenomena are however complicated by the very early appearance of the internal thickening of xylem which ultimately leads to the development of the second (internal) cylinder. This first appears while the stele is still in the *Lindsaya*-phase (Fig. 60 D) and the internal ridge even separates from the

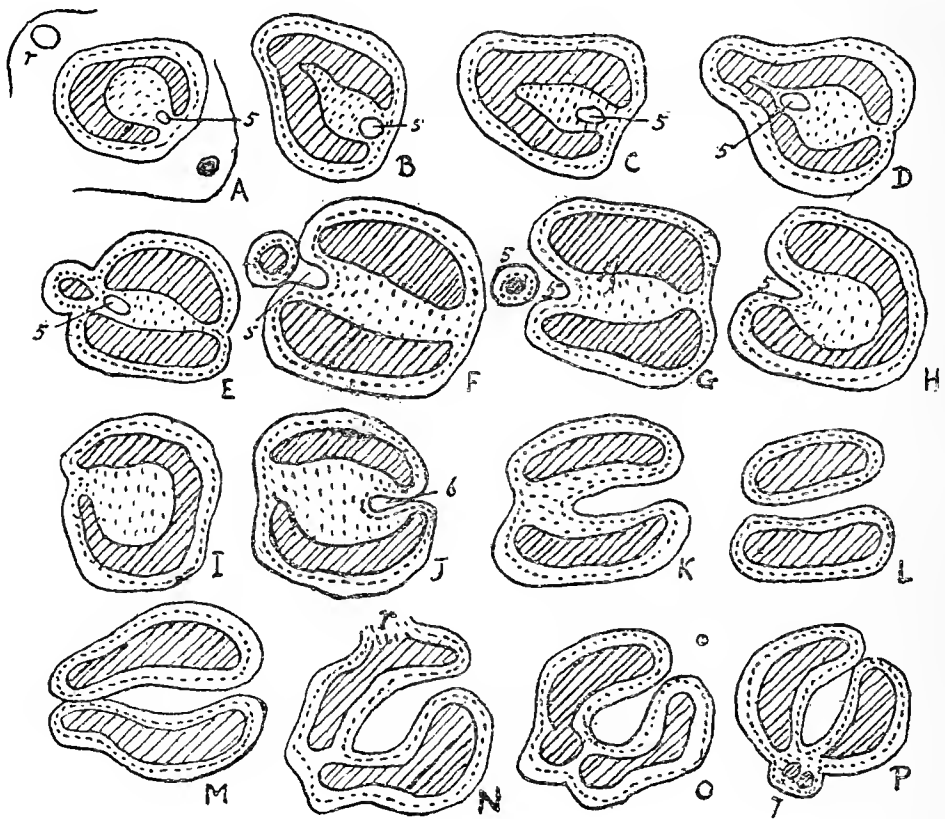


Fig. 100. *Lomeria Spicant*. Ontogenetic evolution of dictyostely directly from the *Lindsaya*-type without the interposition of the solenostelic condition. The ground-tissue pockets (5) and (6) are unconnected with one another. The sixth and seventh leaf-gaps overlap. From Chandler.

main xylem-cylinder and runs free in the internal phloem through part of the internode, joining the external xylem at the next leaf-insertion. When the solenostelic condition is reached this internal strand becomes surrounded by its own phloem, pericycle and endodermis (though it is confluent with the main cylinder for a considerable part of its course), and thus becomes a protostelic accessory internal cylinder. At later stages it successively passes through the *Lindsaya*-phase and the phase with internal endodermis, eventually in its turn reaching the solenostelic condition (Fig. 61, P, Q, T).

The early appearance of the internal accessory strand is probably to be attributed to the "working back" of the polycyclic condition into the very young plant. It is well known that a constant thoroughly established character in an adult organism tends to be inherited at earlier and earlier stages of the life history, and there can be little doubt that this is what has occurred in the present case. We can hardly suppose that the internal accessory strand was present when the ancestors of *Matonia* were in the monocyclic *Lindsaya* condition with a very simple type of leaf-trace. This is a good illustration of one type of the overlaying of the phylogenetic history as recorded in the ontogeny, by the supervening of new or "cœnogenetic" characters as they are sometimes called.

The adult *Matonia pectinata* is still oscillating, so to speak, between the dicyclic and the tricyclic conditions, the third cylinder being a comparatively new development. It only appears in the largest rhizomes and is often discontinuous, but it bears exactly the same relation to the second cylinder as the second does to the first. In correspondence with the increasing size of the vascular system it may exhibit the protostelic, the *Lindsaya*-, or the solenostelic type.

The leaf-trace of *Matonia pectinata* passes through an ontogenetic series of stages starting with a simple iso-diametric strand and ending with the complicated arch with spirally coiled free edges characteristic of the adult form. This series of stages runs *pari passu* with the increase in complexity of the vascular system of the stem, the incurved edges of the trace being entirely supplied by the second internal cylinder. As we saw in the first part of this lecture these incurved ends of the trace are separated in the sympodial branches of the frond as internal accessory strands which contribute to the formation of each successive pinna-trace. Their development is probably to be correlated with the shortening of the sympodial branch-system of the frond and the consequent necessity of supplying the successive "pinnæ" in very rapid succession. It is to the demands of the pinnæ and ultimately of the transpiring lamina that we must look, as has already been indicated, for the ultimate stimulus to the increased complication of the vascular system of the stem.

It is to be regretted that we have as yet but little information as to the gradual increase in complexity of the successive leaf-traces of other ferns with elaborate vascular systems. We may expect that such information would throw much light on the ultimate factors in the evolution of such types.

The foregoing statements are based on rather a narrow range of observations,¹ and in their generalised form certainly admit of exceptions in the exact sequence of events; nevertheless they may be taken as substantially accurate. It is scarcely necessary to point out that the history outlined is exactly that which we have seen reason, on comparative grounds, to believe is true of the phylogenetic development of the Leptosporangiate Ferns. The ontogenetic evidence affords most valuable support to the comparative evidence derived from adult structure in reaching our phylogenetic conclusions, and the Leptosporangiate Ferns certainly furnish a very complete and interesting case of the law of recapitulation.

In the general course of ontogenetic evolution the stele of the adult rhizome is arrested at a higher and higher stage of development as we pass up the phylogenetic series. It is possible to suppose that a kind of reduction may have occurred in certain cases which did not involve the actual degeneration of the adult structure, but simply the arrest of the ontogenetic evolution at an earlier phase than in the immediate ancestors, owing to the requirements of the plant having become simpler. Thus we may perhaps explain the adult structure in the genus *Lindsaya* as being a case of arrest of the ontogeny at a stage earlier than in possible solenostelic ancestors, and this might account for the appearance of such a simple type among the Mixtæ.

In the case of the Marattiaceæ we have a very fairly complete knowledge of the vascular system in the young plants (Farmer and Hill, '02, Brebner, '02). Like that of the Leptosporangiate Ferns it begins as a protostele, but the subsequent phenomena appear, at any rate, to be somewhat different. Instead of the internal phloem appearing in the midst of the xylem of the protostele in connexion with the internal phloem of the leaf-trace, a stage is reached at which the leaf-traces in going off leave the stele crescentic in cross section. The crescentic xylem strand sooner or later becomes covered on the inside with phloem, pericycle and endodermis, and the leaf-traces, at first collateral, later on become concentric in structure. The stele sometimes passes through the condition of a closed cylinder in the internodes, but soon becomes definitely dictyostelic by the overlapping of leaf-gaps.

It is not quite easy to know how to interpret this type of

¹ Leclerc du Sablon, '90, Jeffrey, '99, '02, Boodle, '00, '01, A. Gwynne-Vaughan, '03, Chandler, '05, Tansley & Lulham, '05.

stele. It may be that it merely represents a variant of the typical Leptosporangiate ontogeny, the dictyostelic condition having become so marked in the adult stem that it has worked back into the young plant and follows immediately on the protostelic condition, as appears to be the case in *Polypodium aureum* (Fig. 101). If we take that view it would be a typical instance of an ontogenetic history abbreviated by cœnogenetic modification. On the other

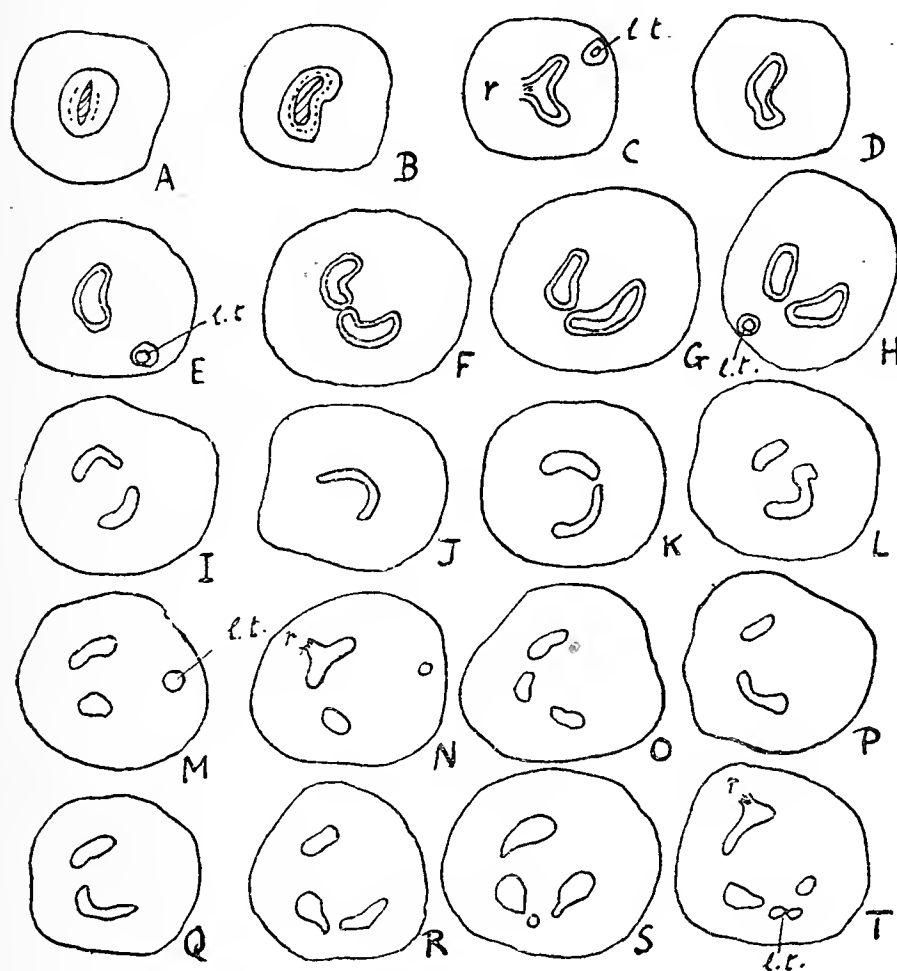


Fig. 101. *Polypodium aureum*. Ontogenetic evolution of dictyostely directly from protostely without a passage through the *Lindsaya*- or solenostelic conditions. The leaf-traces at first single, then double (T) arise from the sides of the leaf-gaps, which are very long. Thus the gap just opening in F, (leaf-trace in H), is closed in P, and the one opening in K (leaf-trace in L, M) is not yet closed in T. From Chandler.

hand it may be held that the Marattiaceæ are a family which have never passed through the *Lindsaya*-phase at all, but have had their dictyostely evolved, so to speak, directly from protostely, the phloem extending round each strand independently. It is to be regretted that we know nothing of the ontogeny of *Kaulfussia*, which has a creeping rhizome and probably represents a more primitive form of adult cylinder than the other genera. The

young plants of the more bulky forms like *Angiopteris* and *Marattia* have more or less elongated stems, so that a primitive type with an elongated axis is distinctly suggested. Such a primitive type may have been solenostelic. On the other hand it may have had a tubular stele without internal phloem, as in the Ophioglossaceæ, and the phloem and endodermis subsequently developed on the internal side of the separate strands. With the evidence at present available it is very difficult to decide between these alternatives.

In the young plants of Ophioglossaceæ, when the cylinder has passed out of the protostelic condition, a pith appears and a distinct internal endodermis is developed. This disappears in the older plants of *Botrychium* and *Ophioglossum*, but remains in *Helminthostachys*, though in a degenerate condition. There is no evidence from the young plants that internal phloem ever existed in the group.

CHLAMYDOSPORE-FORMATION IN THE
BASIDIOMYCETE *PLEUROTUS SUBPALMATUS*.

BY DOROTHEA C. E. MARRYAT.

[PLATE I. AND TEXT-FIG. 1.]

TOWARDS the end of November, 1906, fine specimens of the Basidiomycete *Pleurotus subpalmatus* Fr. were found growing on an old Elm tree in Caius Cricket-ground, Cambridge, where a large branch had been broken off by the wind. Wishing at that time to investigate the wood-destroying powers of various tree Fungi, I made pure cultures of the basidiospores, which were deposited in quantities on laying the hymenium face downwards on clean white paper. The spores were of a fine salmon-pink colour; the medium used for their culture was Gelatine and 10% Grape Extract. They germinated very readily and after about ten days a thin, greyish-white felt-work of mycelium was visible on the glass plates in which the cultures were made.

Sterilised Elm-blocks—sections of which were previously examined microscopically and found to show no trace of fungi—were then infected with small pieces of mycelium from the plate-cultures. The blocks were enclosed in glass tubes plugged with cotton-wool and placed in a dark cupboard.

After three weeks, small cotton-wool-like flecks of mycelium were visible on all the infected blocks, and a fortnight later they were more or less thickly covered with a fine growth of soft flocculent white hyphæ.

At this point, two of the blocks were fixed in absolute alcohol and sections cut of the wood. On examining the latter, a number of curious spore-like bodies were observed, both free and also apparently inside the wood-vessels.

Suspicion being thus aroused, small pieces of the mycelium growing on the blocks were examined, and it was discovered that countless numbers of spores had been, and were being, produced by the hyphæ, the fallen spores being present in such quantities that the latter were almost hidden by them.

It was at first thought that some intruder must have crept into the cultures, but on examining more closely the hyphæ which bore the spores, the presence of numerous “clamp-connections”—

structures highly typical of, and chiefly confined to, the Basidiomycetes—set all doubts on this score at rest. On carefully teasing out small pieces of the mycelium, it was found that the majority of the spores appeared to be produced interstitially at some distance from one another along the length of the hyphæ, after the manner of typical chlamydospores. Sometimes, however, single terminal spores might be observed at the ends of short branches (Plate I., Fig. 7). The spores were thick-walled and colourless, but were filled, as were also the hyphæ, with numerous highly-refractive oil-granules. They varied in size from $12 \times 8\mu$ to $8 \times 6\mu$.

Since it was not easy to tease out the hyphæ of the mycelium very satisfactorily and observe in detail how the spores were being produced, hanging drop cultures were made of them in (α) Water (β) Gelatine and 10% Grape Extract.

These both proved very successful; in the Water hanging drops, the spores began to germinate twenty-four hours after they were sown, sending out short, colourless germ-tubes (Plate I., Fig. 2). The following day these germ-tubes had increased considerably in length (Fig. 3), and on the third day had begun to branch (Fig. 4). By the sixth day interstitial spores or chlamydospores were produced in both the main hypha and its branches. Clamp-connections had also begun to appear (Fig. 5). On the seventh day, the interstitial spores had increased in number, and it was interesting to note that in many cases a spore had been formed immediately beneath the original parent-spore, which, though still attached above, was by this time completely devoid of contents (Fig. 6). At this stage, the water-drops became fouled with Bacteria and it was difficult to make further observations. The Gelatine and Grape-extract drops showed an interesting set of stages in the development of the spores and could be kept for much longer than the water-cultures, but owing to the nature of the medium it was not so easy to follow the course of events under the microscope.

The spores germinated well, but development seemed slower than in the water-cultures and a considerable quantity of repeatedly-branched mycelium was produced—in which the clamp-connections could be seen very beautifully—before any new spores were formed. The latter were not noticed until the tenth day, though later they appeared in considerable numbers. It was often easy to find single spores produced at the ends of short branches, as well as the typical interstitial arrangement; the former are interesting in connection with Brefeld's observations, which will be referred to later.

Plate cultures (Gelatine and Grape Extract) were also made of the spores and a mass of characteristic soft, flocculent white mycelium was eventually produced which bore innumerable spores of the type already described.

Another set of sterilised Elm-blocks was also infected with small pieces of mycelium from the originally infected blocks; this mycelium spread rapidly and in turn produced the typical spores in great quantities. In no case was any trace of the regular hymenial fructification observed.

The cultures were kept under observation for some months, blocks being fixed at intervals for microscopic investigation. After the first two months, however, the mycelium did not appear to be spreading over the blocks very rapidly, though it often collected into little clots, especially at the summit of the blocks, in some cases making its way up in strings as far as the cotton-wool plugs which closed the mouths of the tubes in which the blocks were placed.

On cutting sections of the blocks at different stages of the infection, it was found that the fungus appeared to have only a very slightly destructive action on the wood. For although a number of hyphæ were found to have penetrated into the vessels of the wood, after more than five months the medullary rays appeared practically untouched, though, as seen on staining with Schulze's solution, they were exceptionally full of starch, etc.

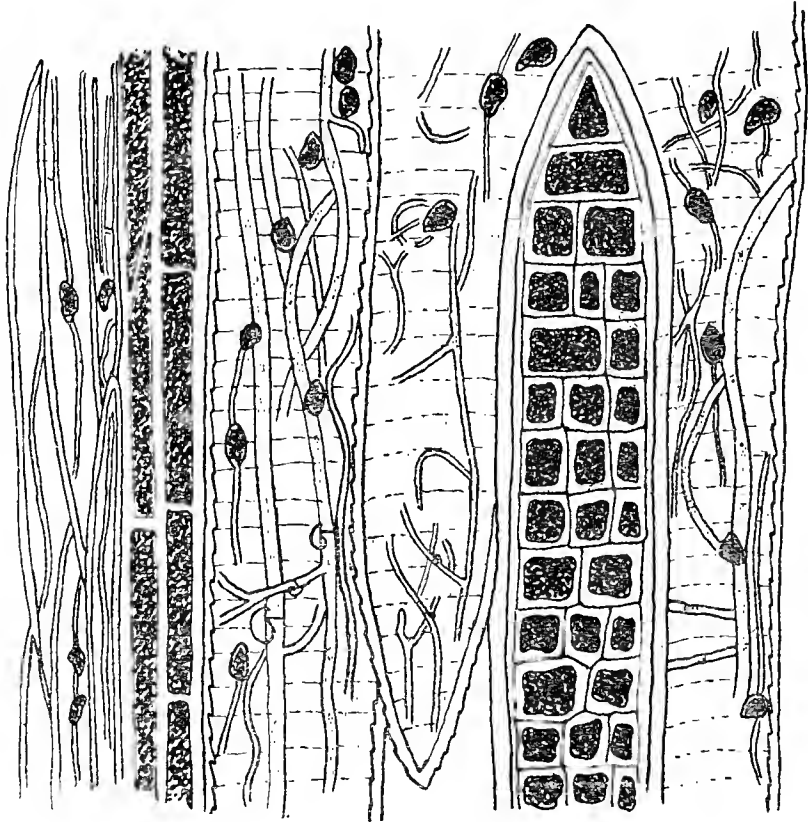
Yet in artificial block-cultures of such a fungus as *Stereum*, Marshall Ward¹ found that the medullary rays were almost the first elements to be attacked, and after some four months were completely invaded and their contents destroyed, by the hyphæ. Further, in *Stereum* the hyphæ are described and figured as passing radially from one tracheid to another through the pits in all directions, whilst in *Pleurotus subpalmatus* this is only comparatively rarely to be observed.

The hyphæ appear to pass into the larger vessels of the wood in considerable numbers, and then to make no further headway, but what is interesting is the fact that they there produce large numbers of chlamydospores, though it is difficult to see of what particular advantage this can be to the fungus (Text-fig. 1). Very good preparations were obtained by staining with Delafield's Hæmatoxylin.

The original object of this investigation was, by using double stains, etc., to endeavour to obtain more evidence as to the destructive effect of the hyphæ upon the lignified cell-walls. For

¹ Phil. Trans., Series B, 1897, Vol. 189, p. 123.

although Marshall Ward,¹ working with *Stereum*, considered that in the infected wood the inner layers of the lignified cell-walls were by the action of the hyphæ converted into cellulose, Potter² later declared that in perfectly sound wood the cells were never all completely lignified, but that when tested some invariably gave the typical cellulose reaction previously attributed to the action of the fungus.



Text-Fig. 1. Tangential section of Elm-block sixty-five days after infection, stained with Delafield's Hæmatoxylin, and showing hyphæ (of two sizes) in the vessels and wood-fibres. The smaller hyphæ are producing numerous chlamydospores, in the larger ones several fine clamp-connections are to be seen.

N.B.—The medullary rays are entirely uninvaded by the hyphæ.

Considering the very slight, or possibly very slow, destructive action of the hyphæ of *Pleurotus* upon wood, it does not appear to be a very suitable species from which to try to collect evidence on this point, though better results may, perhaps, be obtained when the blocks have been infected for a greater length of time.

It seemed, however, worth while to give a short account of the chlamydospore-formation, since it has apparently been only somewhat rarely observed, and I can find no record of these spores having been obtained direct from pure cultures of the basidiospores.

¹ Loc. cit.

² Annals of Botany, 1904, Vol. XVIII., p. 121.

Again, as regards their formation actually within the vessels of the wood, the only parallel cases seem to be the formation of "oidia-chains" (to be referred to below) in the case of *Collybia longipes*, and the innumerable conidia sometimes found in timber infected with *Polyporus sulfureus*. The latter were originally discovered by Hartig,¹ who at first thought that they belonged to some other species of fungus, but mentions them "as he so constantly found them in company with the ordinary hyphæ of *P. sulfureus*." Later Seynes² published a monograph of this species and proved beyond question that this conidial form really belonged to it.

Brefeld³ gives a long and very interesting account of the different forms of chlamydospore already observed in a few genera of Basidiomycetes, and in conclusion his observations may be shortly summarised as follows. The very simplest forms are the so-called "oidia-chains (Oidienketten); these appear to be produced by the simple division of the hyphæ into long chains of cells, and a whole mycelium may sometimes break up in this way. The single limb on germination again produces an Oidia-chain and so on for generation after generation. Examples of this kind of formation have been recorded for various genera such as *Phlebia*, *Irpex*, *Pholiota*, *Hypholoma*, *Collybia*, etc. Brefeld goes on to say that though these "oidia-chains" are the simplest known form of chlamydospores, they are not the only ones. Various oidia-forms, slightly more differentiated than those just described, have been observed, and at length a higher form is reached, to which alone, strictly speaking, the term chlamydospore is applicable. So far the latter have been discovered only in the genus *Nyctalis* amongst the *Agaricini*, and in *Fistulina* and *Oligoporus* amongst the *Polyporei*.

In the first genus, the formation of true chlamydospores appears to be always preceded by the formation of "oidia-chains," in the other two genera the latter are wanting.

It seems that very often the chlamydospores arise in special positions in relation to the true fructification or hymenial layer (cf. Brefeld, Plate VI., Fig. 4), actually appearing in company with the basidiospores. At other times, however, they are borne in great numbers by the hyphæ of the ordinary mycelium. Brefeld further observes that short branches may be sent up into the air on which the spores are borne not interstitially, but *terminally*, which is

¹ Zersetzungsercheinungen des Holzes, p. 112.

² Bull. de la Société Botanique de France. Tome XXXI., p. 296.

³ Untersuchungen aus dem Gesamtgebiete der Mykologie. Heft VIII., p. 203, etc.

interesting in the light of what was noticed in the cultures of *Pleurotus* (cf. Fig. 8). Finally these terminally-borne spores may form tufts indistinguishable from a true conidial form, this being specially striking in the case of *Fistulina*.

Brefeld concludes by endeavouring to trace up in detail the morphological relationships between all these different forms. He gives numerous and excellent figures of the various kinds of spores found in the different species, the chlamydospores of *Nyctalis* (Plate VI., Figs. 12, 13, etc.) bearing a very close resemblance to those described in the present paper.

Cambridge Botanical Laboratory.

November, 1907.

EXPLANATION OF FIGURES ON PLATE I.

The figures are all from drawings made with the aid of a Camera Lucida, and are \times about 500.

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- Fig. 1. Loose chlamydospores filled with oil-drops.
- Fig. 2. Chlamydospores germinating in hanging water-drop after twenty-four hours.
- Fig. 3. Ditto after forty-eight hours.
- Fig. 4. Ditto after three days, the hyphæ are beginning to branch.
- Fig. 5. Ditto after six days, the hyphæ have formed chlamydospores and clamp-connections.
- Fig. 6. Ditto after seven days, showing spores forming immediately beneath the mother-spore, which is now quite empty.
- Fig. 7. Branched mycelium produced from chlamydospores sown in hanging drop of Gelatine and 10% Grape Extract, after ten days. The clamp-connections show well.
- Fig. 8. Spores produced terminally at the ends of short branches; from hanging drop-cultures of Gelatine and Grape Extract, sixteen days old.
- Fig. 9. Spore-bearing hyphæ teased out from small piece of mycelium from infected block.
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THE DISPERSAL OF FRUITS AND SEEDS BY ANTS.

BY F. E. WEISS,

Professor of Botany in the Victoria University of Manchester.

[TEXT-FIG. 2].

BOTH to those who are interested in the biology of plants and to those engaged in the study of plant ecology, Sernander's "Entwurf einer Monographie der Europäischen Myrmekochoren¹," will be a welcome source of information. Already in an earlier Swedish publication² (with German summary) Sernander had distinguished three ways which animals might aid in the dispersal of seeds and fruits. If feeding on succulent fruits they pass the seeds through the alimentary canal, he applies the name of *endozoic* to the method of distribution, while he uses the term *epizoic* for the dispersal of fruits which adhere by means of hooks or sticky glands to passing animals. A third method of dispersal in which animals *intentionally* collect seeds or fruits which they may either let fall on the way or carry to their nests Sernander designates as *synzoic*. As instances of this method he cites the carrying off of nuts and other fruits by certain rodents, and particularly the transportation of small fruits and seeds by various species of ants. It is to a thorough investigation of this latter agency that the recent monograph, running to some 400 quarto pages, is devoted. To describe this particular case of synzoic distribution, Sernander uses the term myrmecochorous (μύρμηξ = an ant; χωρεύω = I wander), a term independently used by Béguinot and Traversa³ in the same sense.

After referring to some of the more or less well-known instances of the dispersal of seeds by ants, such as the observations of Moggridge⁴ and Lubbock⁵ on the seeds of the violet, of Lundström⁶

¹ Kungl. Svenska Vetenskapsakademiens Handlingar. Bd. 41. No. 7. Uppsala 1906. With 11 Plates and 29 Text-figures.

² Den skandinaviska vegetationens spridningsbiologi. Uppsala 1901.

³ Nov. Giornale Botanico Ital. Fireinze, November, 1905.

⁴ Moggridge, J. Tr. Harvesting Ants and Trapdoor Spiders. London, 1873.

⁵ Lubbock, Sir John. Ants, Bees and Wasps. 4th Edition. London, 1882.

⁶ Lundström, A. N. Pflanzenbiologische Studien II. Die Anpassung der Pflanzen an Thiere. Nova Acta Soc. Sc. Upsala, Ser. 3, Vol. XIII. 1887.

on those of *Melampyrum pratense*, of Kerner¹ on *Chelidonium* and others, Sernander proceeds to classify the very large number of other fruits and seeds which he has been able to add to the previously short list of seeds known to be myrmecochorous. The attraction which these seeds have for ants he attributes to the food, largely of an oily nature, which practically all myrmecochorous fruits or seeds provide in more or less accessible form, the supposed mimicry of the pupa of ants by certain seeds, such as those of *Melampyrum* he considers as possibly accidental. The seeds of *Melampyrum* are provided with an elaiosome, the removal of which, as well as of the oil-containing seed-coat retards the collection of the seeds by the ants in much the same way as is the case with other myrmecochorous seeds.

In the most striking, and possibly also the most numerous cases, the seeds are provided externally with definite food bodies or elaiosomes ($\epsilon\lambda\alpha\iota\omicron\nu$ = oil; $\sigma\omega\mu\alpha$ = body), which in the form of crests, caruncles or strophioles are characteristic of certain groups of seeds.² In some plants, however, where no distinct elaiosomes are present, fatty oils are to be found in other parts of the seed, or fruit, or in some other organ connected with the latter. A brief review of the various types distinguished by Sernander will perhaps give the best idea of how the "dispersal-units" are rendered attractive to ants.

We have (1) the *Puschkinia* type in which the delicate seed-coat is impregnated with oil. This group includes besides the above mentioned genus, some Liliaceæ, such as *Allium ursinum*, and several species of *Ornithogalum*.

(2). The *Viola odorata* type in which a portion of the seed forming a strophiole or caruncle is developed as an elaiosome, is probably the largest, as well as the most striking, group of myrmecochorous seeds. To it belong a number of Monocotyledons, such as various species of *Chionodoxa*, *Lachenalia*, *Scilla*, *Galanthus nivalis* and *Luzula pilosa*. Of the Dicotyledons, *Arenaria*, *Reseda odorata*, *Chelidonium majus* and several species of *Corydalis* and *Viola* may be mentioned. In some cases the elaiosome is formed by the crested funicle. This is the case in the seeds of the primrose, in which a portion of the seed-coat also contains oil.

¹ Kerner and Oliver. Natural History of Plants, 1895. Vol. II., p. 866.

² Robertson, Ch. Seed Crests and Mymecophilous Dissemination of Certain Plants. Botanical Gazette, Chicago, 1889.

(3). In the *Hepatica* type the basal portion of the pericarp is transformed into the elaiosome. Examples are *Ficaria ranunculoides*, *Hepatica triloba*, *Fumaria capreolata*.

(4). The *Parietaria* type has the base of the perigone stored with oil.

(5). In the *Ajuga* type the nutlets on separating carry away a portion of the floral axis (pseudostrophiole) which with the base of the pericarp constitutes the elaiosome. Examples :—several Labiatae and Borragineae.

(6). In the *Arenaria* type, to which *Thesium*, belongs the basal portion of the thalamus forms the elaiosome, while this organ is formed by the base of the utriculus in the (7) *Carex digitata* type. Finally in a few grasses the elaiosome is formed by a part of the inflorescence. This constitutes the (8) *Melica nutans* type.

In a number of other cases the plants possess some additional means of seed dispersal besides that due to ants. Thus in *Euphorbia*, where we have an elaiosome of the *Viola odorata* type—the seeds are ejected by dehiscence of capsule. This applies to some of the species of *Viola*. In other cases the fruits are more or less anemochorous, but possess elaiosomes in addition. Thus in several species of *Centaurea* (*C. cyanus*, *C. dealbata*) ridge-like swellings at the base of the fruit are found to contain oil, and these fruits are eagerly sought after by ants. In some species of *Carduus* and *Cirsium* the pappus is lost very early, and the base of the style functions as an elaiosome. These and others constitute five additional types of Sernander.

From the examples mentioned above it will be seen that the European myrmecochorous plants are largely meadow and woodland plants, many of them flowering early in the year and fruiting during the period of insect activity. Of the 120 plants which Sernander claims as myrmecochorous, many show adaptations to this form of dissemination other than the possession of an elaiosome. The greater number are found to have a comparatively poor supply of mechanical tissue in their flowering axis, which, after the flowering period, becomes limp and bends down so that the capsule often opens on the ground. This is the case for example in *Scilla sibirica*, *Anemone hepatica*, *Ranunculus ficaria*, *Viola odorata*, while allied species which are not myrmecochorous produce their flowers on erect inflorescences. Of course in the case of plants which combine anemochory with myrmecochory the fruiting axis always remain erect.

The Swedish naturalist does not base his recognition of these various seeds as myrmecochorous on the presence of recognisable elaiosomes; the great value of his monograph lies in the very careful and detailed experiments by which he supports his contention that the elaiosome is the organ that definitely attracts the ants. In the case of each species of plant he has made and recorded numerous experiments both with normal seeds and with seeds deprived of their food-bodies, and the evidence strongly supports his main thesis as to the attractiveness of the elaiosome.

The question as to the effectiveness of ants in the dissemination of plants Sernander answers by observations made both in the South of France and in Sweden. As regards distance he has seen from direct observations seeds carried 15 to 70 metres; while as to numbers he observed near Montpellier some ants of the genus *Aphenogaster* within three hours carrying 216 seeds. In Sweden during nineteen hours he observed *Formica rufa* carrying 366 seeds and fruits, of which 156 were those of *Melica*, 69 of *Melampyrum*, 31 of *Luzula pilosa*, 28 of *Hepatica triloba*, 25 of *Carex digitata*. Assuming that these ants were at work on 80 favourable days in the year and were to work for twelve hours a day, the total number of seeds transported would be 36,480. Of course many if not most of these seeds would be carried to the nests, around which he often found the seeds thrown out with the elaiosomes bitten off, but many are left on the way, as is well shown by a diagrammatic figure of the occurrence of plants bearing myrmecochorous seeds in the vicinity of an ant hill. To find out the number of seeds dropped by the way Sernander staked out a quadrat (square meter) on a path leading through a wood in which *Melampyrum pratense* was growing. The said path was largely used by the ants at the time when the seeds of the cow-wheat were mature and he counted on his quadrat no less than twenty-eight seeds which had been left behind.

Sernander deals also with the ecology of the myrmecochorous plants, which, as stated above, are largely meadow and woodland plants. He finds them most common in meadow-land and particularly in limestone meadows, representing in some regions of Dalecarlia as much as 40% of the vegetation. The presence or absence of ants therefore would seem to be an ecological factor of no small importance. It is interesting too to note that a large number of the so-called ruderal plants which settle and are found growing upon waste places are myrmecochorous, and this is particularly the case in the Mediterranean region, where no doubt

insect life is more abundant than in Sweden. It is clear from a perusal of Sernander's monograph that too little attention has been paid to this interesting method of plant dispersal and that a closer study of this feature of plant life may explain some of the problems which still puzzle ecologists.

One such problem, first mentioned to me by Mr. Tansley, and to which Mr. Hugh Richardson of York subsequently drew my attention, was the apparent incursion of furze bushes into pure heather moor. A striking example of this is seen on the high moorland between Rievaulx Abbey and Coxwold particularly in the region just above Wass bank. Here numerous bushes of *Ulex* are found on either side of the main road, and also, diverging from the main road, long rows of furze bushes may be seen running a quarter of a mile or so into the *Calluna* moor. A closer examination shows that these rows of furze bushes mark the course of old cart tracks, the ruts of which can still be seen under the heather, particularly where the heather has been burnt off. As the seeds of the furze are provided with a bright orange caruncle containing a large amount of oil (Text-fig. 2) and resembling therefore the elaiosomes of the



Text-fig. 2. Seed of *Ulex Europaeus* (enlarged about ten times) showing caruncle. A., Side view. B., View looking down upon hilum.

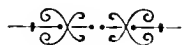
mymecochorous plants, it appears to me that the intrusion of the furze into the heather-moor may be due to the dispersal of the furze-seeds by ants. Ants are known to make use of paths and tracks across a country otherwise difficult to negotiate and they might well have made use of the ruts of the old cart track. As a matter of fact I found ants, and even a small nest, in one of the old ruts in which seedlings of *Ulex* were also found. Unfortunately I was unable to make investigations on the spot as to an actual dispersal of the *Ulex* seeds by ants. Experiments made with ants in captivity have not been very conclusive, for though in some cases they carried away and buried the seeds provided for them, they often left them untouched. However they also neglected the

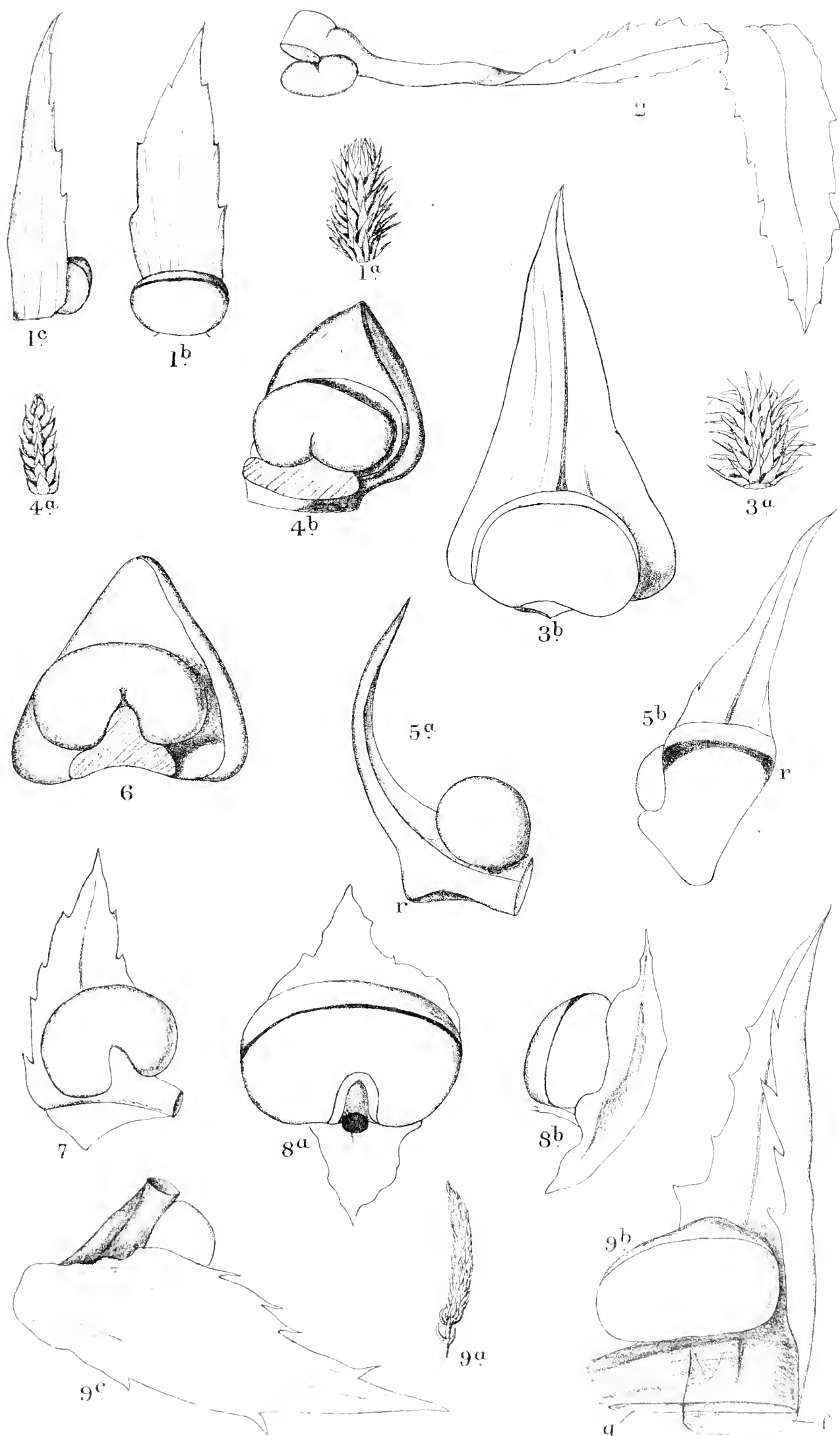
seeds of *Viola odorata* and *Chelidonium majus*, which are known to be myrmecochorous. I propose to make definite observations on this point next summer but I mention the problem as one which seems to be open to solution from the experimental point of view and along the lines of Sernander's useful and important observations.

There remains one point to be noted with regard to the dispersal of plants by ants, and that is the fact that some species of ants such as *Aphenogaster barbara* and *Aphenogaster structor* collect and carry away indiscriminately all seeds that are not beyond their powers of transportation. They do not confine themselves to those which have elaiosomes, but take away to their nests other fruits, such as those of *Anthoxanthum odoratum*, *Festuca ovina*, *Betula alba*, *Anemone nemorosa*. For what purpose this is done remains at present a mystery. Possibly they germinate them and feed on the seedlings. These fruits show no adaptation to transportation by ants and the problem for solution is rather of interest to the zoologist than to the botanist. In the case of the seeds provided with elaiosomes, it is obviously this organ which is sought for by the ants, for seeds divested of their elaiosome are often found thrown out from the ant-hills.

The above account of Sernander's extensive and painstaking investigation will indicate sufficiently the value and interest of his monograph and may be of use in drawing attention to one aspect of plant distribution, which has up to now not received sufficient attention, but which is obviously of greater importance than was formerly supposed.

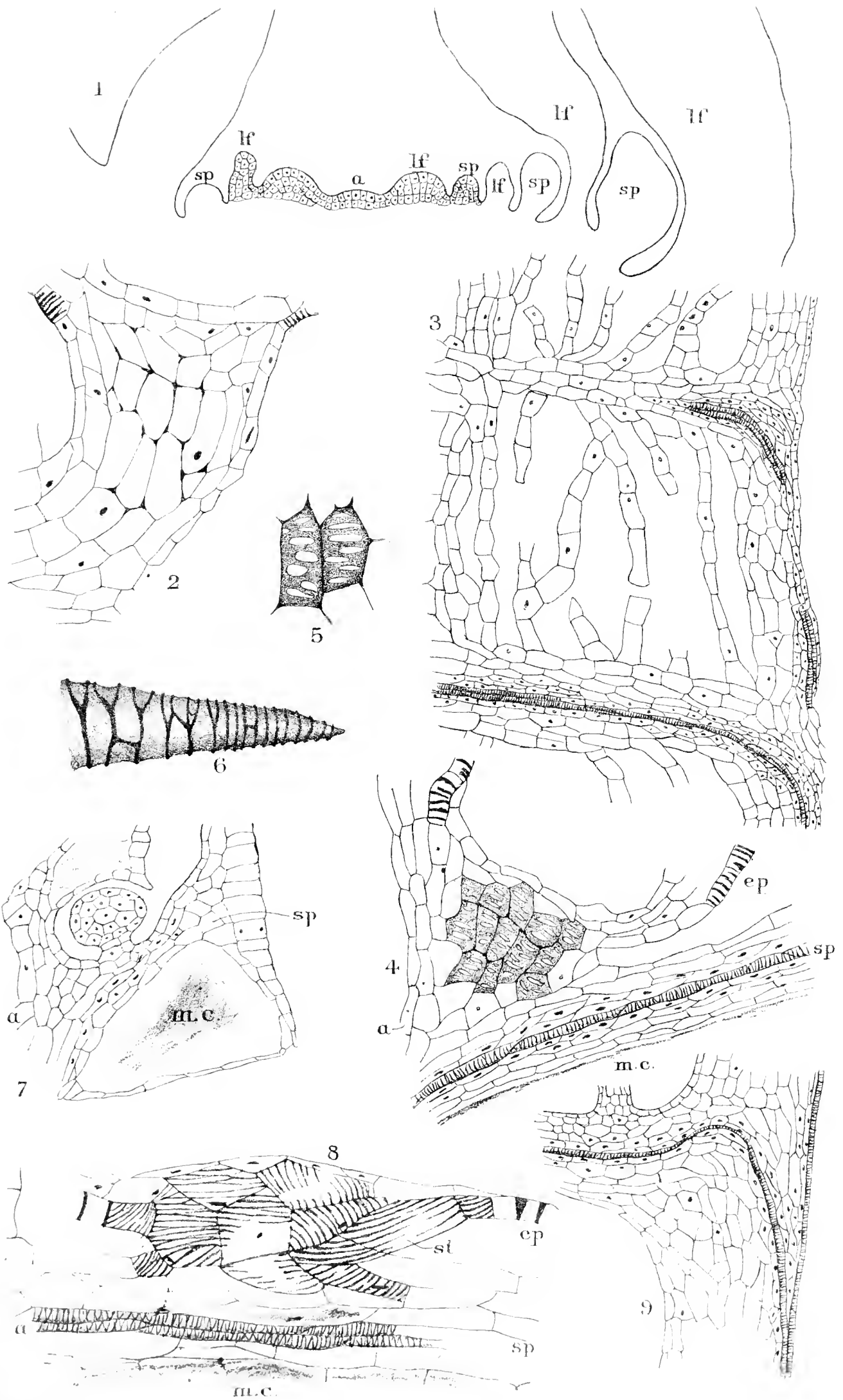
January, 1908.





M. G. Sykes, del.

Highly magnified



M.G. Sykes, del.

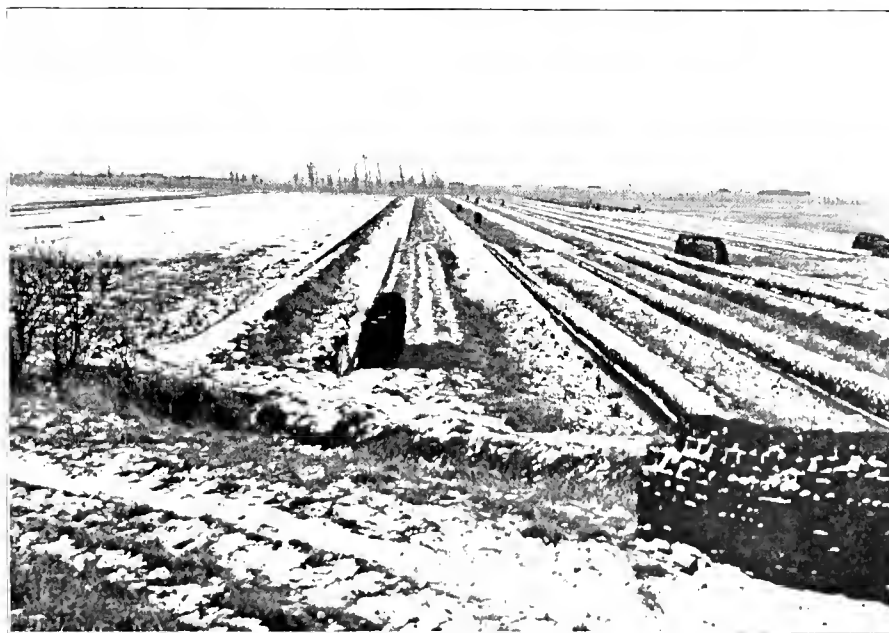
Higley, lith. et imp.



Fig. 1.



Fig. 2.



R. H. Y. photo.

Fig. 3.

YAPP WICKEN FEN.

THE
NEW PHYTOLOGIST.

VOL. VII., Nos. 2 & 3

MARCH 31ST, 1908.

LECTURES ON THE EVOLUTION OF THE
FILICINEAN VASCULAR SYSTEM.¹

BY A. G. TANSLEY, M.A.

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LECTURE X.

A COMPARISON OF THE VASCULAR SYSTEM OF THE FERNS WITH
THAT OF OTHER PHYLA OF VASCULAR PLANTS.

WE are undoubtedly justified in concluding that the primitive vascular system of the shoot of vascular plants is what has been called a protostele, *i.e.*, a solid strand of tracheal-tissue with or without intermixed parenchyma, typically circular in transverse section, surrounded by phloem and probably also by pericycle and endodermis. This conclusion is pointed to, first by the occurrence of this type of cylinder (1) among the Lycopods, particularly in the earlier Palæozoic forms,² (2) among the Psilotales, (3) in the Sphenophyllales, (4) among those Leptosporangiate Ferns which we have other reasons for regarding as primitive. Secondly it is pointed to by the occurrence of the protostele in the young plants of practically all Pteridophytes that have been investigated. Thirdly we have the evidence derived from its occurrence in the gametophyte of the Mosses (in the form of a simple compact strand of water-conducting elements which may or may not be surrounded by a specialised tissue for conducting soluble organic substances), and in the thallus of a few Liverworts. These Bryophytic gametophytes, though of course they have no phylogenetic connexion with the

¹ A Course of Advanced Lectures in Botany given for the University of London at University College in the Lent Term, 1907.

² See especially Kidston, On the Internal Structure of *Sigillaria elegans* of Brongniart's "*Histoire des végétaux fossiles.*" Trans. Roy. Soc., Edin., 41, Part III. (23), 1905, p. 548.

sporophytic plant-body of the Vascular Plants, yet realise pretty closely in the one case the life-conditions of simple terrestrial microphyllous plants, and in the other those of simple terrestrial plants in which certain branches of a generalised thallus are tending to become specialised for assimilating functions—plants of a type which we have seen reason to believe may have been the ancestral type of the megaphyllous vascular forms. These converging lines of evidence are full warrant for the doctrine of the primitiveness of the simple central type of stele,¹ apart altogether from *a priori* considerations, into which we cannot enter here, but which appear to give ample ground for expecting what we actually find, that primitive conducting tissue tends to be developed in the centre of an axial plant-body.

The subsequent evolution of the protostele depends very largely on the relation to it of the leaf-trace. The leaf-trace itself was also no doubt primitively a simple strand of conducting tissue, whose size would naturally depend upon the size of the leaf. If the leaf is primitively a branch of a dichotomous thallus the departure of the leaf-trace from the stele is primitively a forking of the stele into two equal or nearly equal branches; if it is a lateral member, originally of the same morphological category as the stem from which it arises, the branch of the stele may be expected to show an identical structure, but a lateral insertion; and finally if the leaf is a relatively small appendage to the stem its trace will be a relatively small appendage to the cauline stele, connected directly only with the external tissue of the latter. Of course it is conceivable that any one of these conditions might arise in the course of evolution from either of the others by a gradual modification of the relation between axis and leaf.

As we saw in the first lecture the available evidence does not enable us to decide the question, so far as the Lycopods are concerned, as to whether the last condition is primitive or has arisen from a state in which the leaves were more important in relation to the stem. But there is some reason to suppose that the Equisetales, Sphenophyllales and Psilotales, as we mainly know them, are reduced from forms with larger dichotomously branched leaves, though we have no sufficient information as to the relation between stele and leaf-trace in such forms.

¹ Brebner's term *haplostele* is better than protostele when we wish to describe this structure without morphological implication. In some cases no doubt a haplostele is not a protostele, but has arisen by reduction from a more complex type of structure.

Professor Jeffrey, as is well-known, has proposed to divide the Pteridophyta into two primary groups: the *Lycopsida* or palingenetically microphyllous forms, in which the departure of the leaf-trace does not leave a gap in the stele, and which includes all the phyla just mentioned; and the *Pteropsida* or palingenetically megaphyllous forms, in which the departure of the leaf-trace does leave a gap in the central cylinder when this is siphonostelic in structure, and which includes the Ferns, Ophioglossales, Pteridosperms, Gymnosperms and Angiosperms. "These two great stocks" says Jeffrey, "appear to have been separate back to the beginning of the period when the palæontological record begins" ('02, p. 144). This statement, with certain qualifications, is no doubt true, but nevertheless the grounds of the fundamental distinction proposed by Jeffrey appear open to a certain amount of criticism.

In the first place the evidence now rather tends to the conclusion, as was pointed out in the first lecture, that many of the modern microphyllous forms are reduced derivatives of megaphyllous ancestors. At any rate it is a striking fact that a large number of the Palæozoic forms had dichotomously branched leaves. Whether or no the Ferns have any direct connexion with these forms is another matter, but the supposition that the "*Lycopsida*" are all palingenetically microphyllous is certainly an assumption which lacks justification.

With regard to the anatomical distinction, there seems to be no escape from the view that the anatomical relation of leaf-trace and stele must depend first upon the actual size of the leaf-trace in relation to the stele, and secondly upon the construction of the stele itself. The departure of the small leaf-traces from the stele of a Lycopod or of a Sphenophyllum leave no gaps in the stele, whether the xylem of the latter is solid or medullated; in the latter case because they are too small to affect the whole breadth of the xylem ring.

Professor Jeffrey has nowhere discussed in detail the origin of the siphonostele from the protostele, though he himself ('98) stated the view of the primitiveness of protostely. In the *Gleichenia*—*Lindsaya*—*Wibelia* series (Lectures I V & V) the origin of phyllosiphony certainly goes hand in hand with the origin of solenostely, but in the Osmundaceous series discovered by Kidston and Gwynne-Vaughan the origin of a hollow stele is clearly shown to be unconnected with phyllosiphony.

In the medullated *Lycopsida*, as has been said, the departure

of the leaf-trace leaves no gap in the stele because in relation to the breadth of the xylem ring the trace is too small to cause an interruption in the tracheal cylinder. In *Tmesipteris* however it appears, from the recent investigation of Miss Sykes¹, that the sporophyll-traces, or as she would consider them "branch-traces," do make a gap in the xylem on leaving the stele, while the traces of the sterile foliage leaves do not. Professor Jeffrey might consider this fact conclusive evidence that the bifurcate "sporophylls" are really branches, but Miss Sykes shows that the traces of the two kinds of organs leave the stele in essentially the same way and that the difference between them in the matter of gap-formation is of one degree only. Furthermore Professor Bower ('08) has recorded a case in the upper part of the sterile region, in which the traces of sterile leaves are associated with gaps in the xylem ring.

Again, the affinities of the very isolated Ophioglossales, which on Jeffrey's test would fall into the Pteropsida, are quite doubtful, but the balance of evidence tends to connect them with the sporangiophoric, *i.e.*, "Lycopsid," types rather than with the Ferns.

Thus the most that can be maintained is that in the vast majority of the forms belonging to certain groups which are typically protostelic and whose modern representatives at least are typically microphyllous, the leaf-trace is attached only to the external layers of the xylem and its departure makes no gap, while in the majority of certain other, typically megaphyllous, groups a broad tubular type of stele—not found in the primitive types of the same groups—has been evolved, and the large leaf-trace is attached to the whole breadth of the xylem ring so that the continuity of the hollow cylinder is interrupted at the departure of the trace. Once such gaps have been formed they play an essential part in the general construction of the stele, so that in the higher types—the higher Ferns and the great seed-bearing series—the constituent strands of the leaf-trace appear as springing from the sides of the long and wide gap, instead of seeming to "cause" the gap, as in the middle (solenostelic) types. An analysis of the factors involved in gap-formation has already been attempted in the fifth and ninth lectures.

The whole question resolves itself into the actual size-relations of leaf-trace and stele in any given form, as modified by the ancestrally determined construction of the stele itself. Thus a

¹ M. G. Sykes. The Anatomy and Morphology of *Tmesipteris*,
Ann. of Bot., Vol. XXII., 1908.

reduced form like a *Vittaria* is phyllosiphonic, though if its immediate ancestors had been protostelic no leaf-gaps could have been formed. If the reduction of leaf-traces *relatively to the stele* is great enough, a siphonostelic form like *Platyzoma* may have no leaf-gaps. And in a type like *Tmesipteris*, which is no doubt reduced, but in which the leaf-trace has a considerable importance in relation to the size of the stele, leaf-gaps may or may not exist.

THE MORPHOLOGICAL CONSTRUCTION OF SELAGINELLA COMPARED
WITH THAT OF THE FERNS.

Enough has now been said as to the relations between the Ferns and the modern microphyllous forms in general, but the striking vascular system of the genus *Selaginella* presents a very interesting case of analogy with that of the Ferns, and to this analogy it will be useful to devote a little consideration.

The "gross anatomy" of the vascular system of the shoot axes of *Selaginella* is strikingly variable within the genus,¹ which indeed presents a range of vascular structure not only unequalled among other Pteridophytic genera, but almost comparable with the range exhibited by the whole phylum of Leptosporangiate Ferns.

The points of resemblance between *Selaginella* and the Ferns are numerous and striking. With the exception of the Ferns, *Selaginella* is the most successful Pteridophytic stock in the modern world. The five hundred known species inhabit for the most part the forests of the damp tropical region. Here they are very abundant not only holding their own in the struggle with angiospermous types but frequently dominating the ground vegetation over considerable areas. Some species are positively weeds in many of the wayside ditches and on damp banks bordering the roads in the Eastern Tropics. The species are also very polymorphic and often difficult to separate, a common sign of actively progressive evolution.

In habit the dorsiventrally organised aerial branch-systems of many species strongly resemble the typical repeatedly pinnate fern-frond. Each axis of this branch-system bears four rows of leaves, the leaves of the two ventral rows standing out on each side of the stem in the plane of the branch system, while the smaller leaves of the two dorsal rows lie flat upon the upper surface of the stem. The whole branch-system with its leaves, like the pinnæ of a fern-frond,

¹ R. J. Harvey Gibson. Contributions to the Anatomy of *Selaginella*. I.—The Stem. Ann. of Bot., Vol. VIII., 1894.

often tends to form a continuous plate of foliage or "leaf-mosaic." This frond-like structure, in certain species, assumes a gentle curve, so that most of its surface is approximately horizontal and receives at right angles the relatively weak light reaching the tropical forest floor.

When we turn to the vascular system we find that many of the species are what has been called "polystelic," and in this case with much more justice than in the Ferns.

In the European species, *S. spinosa*, the stele is typically Lycopodinean and the whole stem is radially organised. In *S. Martensii* there is a simple diarch band-shaped stele, the two edges of the band being lateral and occupied by protoxylem strands, to which the traces from the dorsal and ventral leaves on each side are attached. In the larger species with very copious branching of the "frond" the originally simple stele "gives off" similarly shaped accessory structures on both dorsal and ventral sides, in somewhat the same way that the hollow cylindrical stele of a polycyclic fern "gives off" internal accessory strands. As the upper regions of the "frond" are approached the "steles" diminish in number and the ultimate branches contain only a single band-shaped strand.

Here then we see an elaboration of the simple stele to meet increasing complexity of the assimilating branch-system, just as in the Ferns we find elaboration to meet increasing complexity of the frond, but carried out on totally different lines. In *Selaginella* we have a very old if not a primitively microphyllous stock which modifies whole branch-systems for assimilating purposes. The leaf itself is so small as to exercise no influence on the general conformation of the vascular system, and corresponds physiologically with the ultimate pinnule or segment of the lamina in a fern-frond. But the branch-system as a whole retains its plasticity, and becomes moulded on lines parallel with those of the fern-frond as a whole.

In some species there is a creeping underground stem or rhizome sharply differentiated from the aerial assimilating "fronds," and here the parallel with a Fern is carried even further. In one species, *S. Lyallii*, this rhizome actually possesses a typical Filicinean solenostele, the gaps in which are formed by the departure of aerial branch-traces instead of leaf-traces. And further there is an internal accessory vascular strand, free in the internodes, but coming into connexion with the edges of the branch-gap, so that this remarkable form actually imitates the beginnings of typical Filicinean polycyclus.

In the frond-like dorsiventral type of branch-system seen in some species of *Selaginella* we have in fact a kind of working model of the hypothetical thallus of the "pro-Lycopod" alluded to in the first lecture, the leaves representing the ultimate assimilating branchlets, and the whole showing a convergence with a fern-frond hypothetically derived by integration of a whole thalloid branch-system. But whether the Lycopod leaf be an ultimate assimilating branchlet, and whether the fern-frond be an integrated branch-system increase of a thallus, or not, both systems are capable of considerable in complexity and modification, both of external form and in vascular structure, and both have apparently found in this plasticity the means of successfully establishing themselves, though in comparatively subordinate positions, in the struggle with the flexible angiosperms.

THE FERNS AND THE SEED-PLANTS.

Finally, let us briefly compare the Ferns with the great group of the Cycadofilices which lead up to the Cycadophyta and the Flowering Plants.

The seed-bearing fern-like plants are undoubtedly derivatives of the great megaphyllous fern-stock, though they must have branched off from the true ferns long before the rocks were laid down in which the earliest records at present available are enshrined. Nevertheless, since the possible lines of evolution from any given point are limited, we find among the primitive Ferns fairly close parallels with the structures whose evolution marks the beginnings of the lines of descent some of which culminated in the production of the typical vegetative structure of the Flowering plants.

In the first place let us consider the series *Heterangium*, *Lyginodendron*, *Poroxyton*, Cycads, the demonstration of which by Scott was the first convincing proof of the possibility of the evolution of the vascular skeleton of the higher plants from something like that which we find in the more primitive Ferns.

What are the essential features of this progression? First there is the disappearance of the central primary xylem involving the localisation of the xylem of the stele in peripheral strands which are directly continuous with petiolar strands, *i.e.* are leaf-traces. Secondly there is the change of these peripheral strands from mesarch to endarch structure. Thirdly there is the increase in importance of the secondary xylem relatively to the primary, till in

the Cycads the latter is represented merely by a number of protoxylems from which the cambium starts its activity.

The lower members of the series can be paralleled among the primitive Ferns. We have already seen how a solid mesarch stele like that of *Gleichenia* might easily be derived from a simple endarch stele like that of *Botryopteris*, by enlargement and independent decurrency of protoxylems from the leaf-traces. The primary wood of *Heterangium* is almost exactly like that of *Gleichenia*, except that the peripheral groups of xylem corresponding with the leaf-traces tend to be more individualised and the leaf-traces themselves pass off as isodiametric instead of as arched strands. In *Lyginodendron* the primary wood is confined to the leaf-traces and compensation-strands, and the same is true of *Osmunda*. But while in the former plant a considerable amount of secondary xylem was formed, the Fern never acquired this habit, and consequently, like all plants which have no secondary thickening is entirely dependent on the putting out of adventitious roots from the stem. This of course is the real cause of the strict limitations of the Fern type of structure. Directly continuous secondary thickening has been initiated in both the ascending and descending axis, the erect stem is able to grow indefinitely in height, to branch and increase its transpiring surface, because it is able *pari passu* to increase its absorptive surface and its conducting channels. The subsequent history of the evolution of the vascular system of the stem is mainly a history of the perfecting of the mechanism of secondary thickening and of the increasing differentiation of the secondary tissue.

The petiolar strand, at first fern-like (*Heterangium*, *Lyginodendron*) separates into bundles in the higher types, but all along it lags behind the cauline system in progress and is still mesarch in the Cycads. This is in striking contrast to the state of things we have found everywhere in the Ferns, in which the leaf-trace always leads, and the cauline cylinder follows. The reason of this contrast appears to be that in the Cycadofilicinean series the dominant influence is adaptation to secondary thickening of the axis, the condition of the production of an unlimited number of leaves, rather than elaboration of the individual leaf, and though the Cycads retain the fern-like habit, and the typical fern-like leaf-trace curve, leaf-reduction is found in *Poroxylon*, *Cordaites*, and the Angiosperms.

Those Cycadofilices which stand apart from the main series may all be regarded as more or less futile experiments in trying to graft secondary thickening on to the more complicated forms of

Filicinean vascular system. *Sutcliffia*, *Medullosa*, *Colpoxylon*, *Cladoxylon*, *Ptychoxylon*, all tried secondary thickening in conjunction with more or less unwieldy primary systems, mostly clumsy imitations of fern-types. In most of them the secondary tissues of one cylinder or part of a cylinder came into collision, so to speak, with those of another. In none is the primary tissue confined to the simple circle of leaf-traces and compensation strands, which is the condition for rapid growth of the primary shoot, established and made good by the zone of secondary wood. It may be, as Worsdell supposes, that the *Medullosa*-type, by means of a drastic reduction, had a partial success in the evolution of the Cycad-type, thus arriving at a similar arrangement by another route.

The vascular structure described, together with the evolution of the seed, and the ultimate acquirement of siphonogamy and angiospermy, may be regarded as marking the final stage in the long process of progressive adaptation to terrestrial life, and as providing the equipment necessary to the attainment of that complete dominance of world-vegetation reached by the modern dicotyledonous tree.

GLOSSARY

of the principal terms used in these lectures relating to the construction of the stelar system, with references to their original use.

Haplostele. The cauline vascular cylinder in its simpler form, in which the centre is occupied by xylem, and this is typically surrounded by phloem, pericycle and endodermis. (Brebner '02).

Protostele. A haplostele which is assumed to be primitive. (Jeffrey '97).

Amphiphloic protostele (or haplostele) = The *Lindsaya*-type of stele. A stele in which the solid central xylem is traversed by a continuous internal strand of phloem, connecting with the external phloem at the nodes. (Chandler '05: see also Tansley and Lulham '02).

Solenostele (as defined by Gwynne-Vaughan). A stele in which the vascular tissue is arranged in a hollow cylinder with phloem and phloeotermata on either side, the complete continuity of which is interrupted only by the departure of the leaf-traces; the gaps thus produced being closed up in the internode above before the departure of the next

leaf-trace. (Gwynne-Vaughan '01 ; see also Van Tieghem, *Traité de Botanique*, 2^e ed., Tome 2., p. 1372, 1891).

Solenostele (as used in these lectures). A stele in which the vascular tissue is arranged in a hollow cylinder of xylem, lined within and without by phloem, pericycle and endodermis, the continuity of which is interrupted by leaf-gaps which do not overlap.

Perforated Solenostele. A solenostele in which gaps other than leaf-gaps occur. (These lectures).

Dictyostele. A stele in which the hollow cylinder of the solenostelic type is interrupted by leaf-gaps which overlap. (Brebner '02).

Perforated Dictyostele. A dictyostele in which gaps, other than leaf-gaps occur. (These lectures).

Dissected Dictyostele. A perforated dictyostele in which the strands of the stelar network are reduced to thin threads. (These lectures).

Meristele. The individual vascular strand of a perforated solenostele or of a dictyostele. (Brebner '02, not Van Tieghem).

Monocycly. The condition of a stem which possesses a single stem cylinder, whether haplostelic, solenostelic or dictyostelic. (These lectures).

Polycycly. The condition of a stem which possesses accessory vascular strands or cylinders in addition to the principal cylinder. (These lectures).

Di-, Tri-cycly. The condition of a stem which possesses two or three concentric vascular cylinders. (These lectures).

NOTE.—The use of the terms *polystely*, *gamostely*, *dialystely* should be discontinued altogether, so far at least as the ferns are concerned. No phenomena are known in the Filicinean series corresponding with these concepts.

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NOTES ON THE MORPHOLOGY OF THE SPORANGIUM-BEARING ORGANS OF THE LYCOPODIACEÆ.

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[WITH PLATES II. AND III.]

THE cones of several of the species described below were kindly sent by Mr. E. C. Jones, at the request of Professor Seward; others were obtained from material collected by Professor Yapp in the Malay Peninsula, by Mr. Stanley Gardiner in Fiji, and by Dr. Benson in Fiji, while Professor Weiss was so good as to supply me with specimens of *Phylloglossum*. Most of the plants examined were preserved in spirit, but, in a few cases, herbarium specimens alone were available; the double stain, iodine green and eosin, was chiefly employed.

My thanks are due to Professor Seward, both for obtaining material for me, and for his kind interest in my work.

I.—GENERAL DESCRIPTION OF A LYCOPODIAN SPOROPHYLL.

Each sporophyll is a leaf-like organ, more or less modified in accordance with its special functions, and bearing a single, stalked, tangentially placed sporangium, the position of which varies in the different species in its relations to the sporophyll and the main axis. The vascular bundle which supplies the sporophyll arises some distance below its base, from the stele; it pursues an obliquely upward course into the stalk, and traverses the whole length of the sporophyll, but does not give off a branch to the sporangium pedicel. In the latter, however, some cells with lignified walls are usually found, these cells often resembling in character those of the layer surrounding the stele in the axis of the cone.

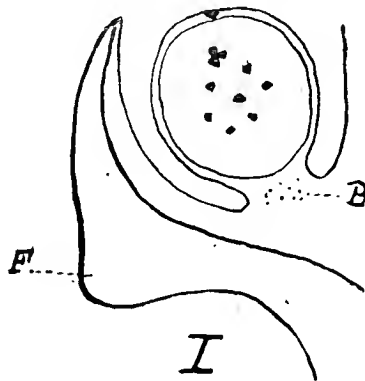
The sporophyll encloses and protects the sporangium to a varying extent in the different species; its epidermis, especially on the abaxial surface, is usually composed of cells with strongly cuticularised walls; a mucilage cavity is often found in its basal portion; it may or may not be furnished with a flap which extends downwards from its dorsal surface¹ and protects the sporangium immediately below, giving to the sporophyll a peltate character.

¹ Goebel, *Organography* II., p. 503.

The sporangium dehisces by a longitudinal slit, along a line of cells which constitute a more or less definite annulus,¹ the position of which varies in the different species.² The wall of the sporangium is composed of two or more layers of cells, which generally increase in number towards the base of the sporangium, and a tapetum. The cells of the outer layer have their walls lignified in unequal strips. In a radial section of the cone the sporangium is a simple oval in shape, but in a section tangential to the axis, the sporangium is much elongated and is usually described as "saddle-shaped."

II.—GENUS I. PHYLLOGLOSSUM.

The cones of this genus have already been described by Bower.³ It is only necessary to remark here that the sporophylls differ slightly from the vegetative leaves, and that they are aggregated to form a definite cone. Each sporophyll is short and simple, rather thick, with incurved edges and a very short dorsal out-growth (Text-fig. 3) which partly protect the sporangium.⁴ It strongly



Text-fig. 3. Longitudinal section of sporophyll of *Phylloglossum*; shewing axillary sporangium. F., Small dorsal flap of sporophyll. B., Lignified cells in sporangium pedicel.

resembles that of *L. dalhousianum* (Pl. II., Fig. 4b), also, more remotely, that of *L. inundatum*, (Text-fig. 5). The sporangium arises in the axil of the sporophyll, but does not fit closely into the base of the sporophyll immediately above; a considerable portion of the sporangium is thus left exposed. Dehiscence of the sporangium takes place by an apical longitudinal slit.

A longitudinal section (Text-fig. 3) shews that the sporangium is borne on a short stalk in which a few cells with slightly lignified walls are often present.

¹ Goebel, Organography, II., p. 579, and cf. Smith, 1900.

² Engler and Prantl, Teil I., Abt. 3, pp. 586 and 587.

³ Bower, 1885.

⁴ cf. Engler and Prantl, Teil I., Abt. 3, p. 576, Fig. 362 c.

III.—GENUS II. LYCOPodium.

I propose to follow Engler and Prantl's¹ classification of the genus *Lycopodium*, for, although this was chiefly based on external characters, it is interesting to find it generally firmly supported by the more minute study of the sporangium-bearing organs. Baker's arrangement², is found to be far less useful for the present purpose.

A. *Urostachya*, [Selago and Phlegmaria (Baker)].

(i) a. *Euselago*. It is characteristic of this group that any or all of the leaves may be fertile; the sporophylls are closely similar to the vegetative leaves and are not aggregated to form a definite cone. Fig. 1A, Pl. II. is drawn from the apical region of a plant of *L. selago*, showing the simple, crowded sporophylls, bearing sporangia which have no special protective apparatus but are exposed between the sporophylls. The drawings of separate sporophylls of *L. selago*, (Pl. II., Fig. 1. B, c) and *L. serratum*, (Pl. II., Fig. 1), show still more clearly the unprotected condition of the sporangium.

The position of the young sporangial rudiment was studied at the apex of a young plant of *L. selago*, (Pl. II., Fig. 1). It is seen that the young sporangium can here hardly be looked upon as foliar in origin, for it appears to arise from the meristematic tissue of the cone-axis in the axil of the sporophyll. Owing to the growth, later, of all the tissues except those between the sporangium and the leaf immediately below it, these two organs appear in the adult far more obviously associated than they were when young.³

The sporangia of the species belonging to this group are all large and are borne on stalks of varying length; these being shortest in *L. selago*, moderately long in *tetragonum*, *fontinalis*, and *lucidulum*, and much more elongated in *quadrangulum*, *dichotomum* and *serratum*. In every case the sporangium dehisces by means of an apical longitudinal slit. A mucilage cavity in the base of the sporophyll is present in several of the species (*selago*, *serratum*, *lucidulum*, *tetragonum*). In the sporangial stalks of *L. serratum* (Pl. III., Fig. 2), and *L. lucidulum*, the walls of some of the cells are found to be more or less lignified,⁴ thickened at the corners, and

¹ Engler and Prantl; Pflanzenfamilien. Teil I., Abt. 3 (Pritzel).

² Baker. Fern-allies p. 7.; cf. Hooker and Greville, Botanical Miscellany, Vol. II., p. 360, and Spring, Mem. de l'acad. royale de Belgique, XV. and XXIV.

³ cf. Selaginella; Bower, 1908, p. 316, Fig. 162.

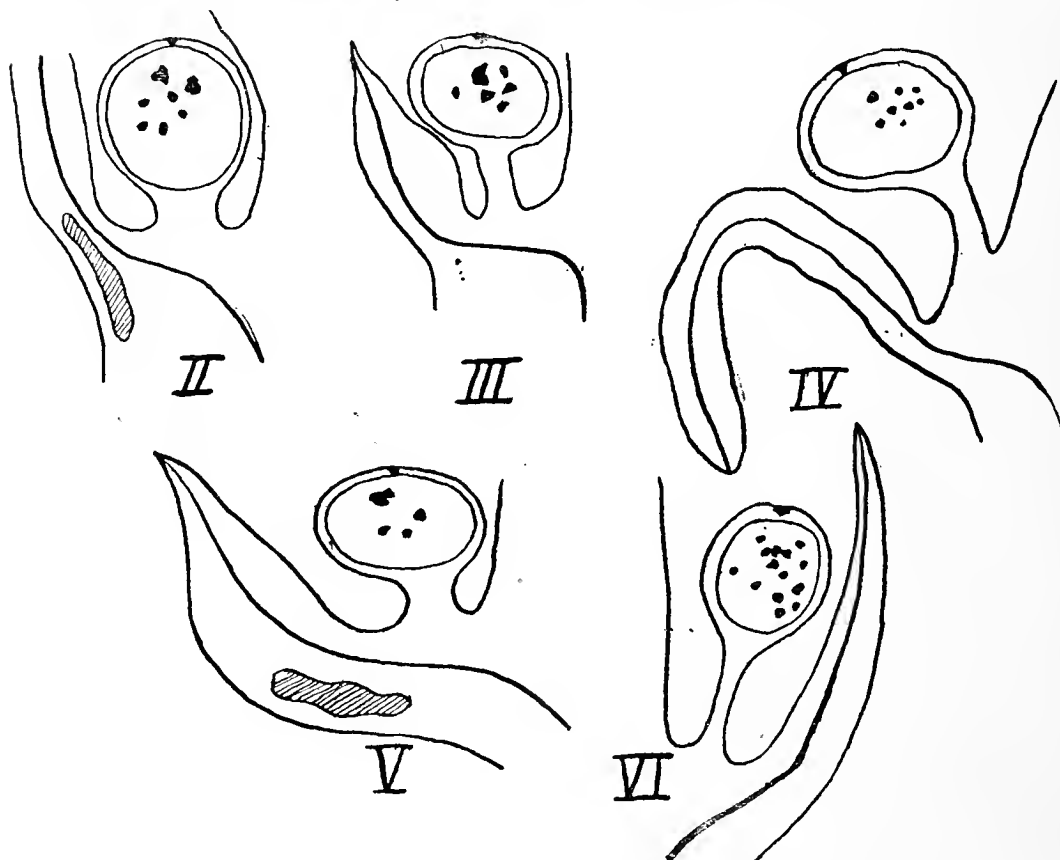
⁴ cf. Cells of sporangial stalk in *Bothrodendron mundum* (D. M. S. Watson, Brit. Assoc. Leicester Meeting, 1907; similar cells are also indicated in Miss Berridge's preparations on the sporangium pedicel of *Spencerites*).

elongated longitudinally in the direction of the axis of the stalk; no connection can however be traced between these and the sporophyll bundle.

The cortex of the stem in *L. selago* is composed of loose spongy tissue, reminding one of the cortex of some *Lepidodendra*,¹ Pl. III, Fig. 3.)

(b). *Subselago*. In this group the upper leaves only are fertile; the sporophylls differ slightly from the vegetative leaves, forming an indistinct terminal spike.

L. squarrosus and *L. dalhousianus* were examined. The sporangia of both are large, and axillary in position. In the former species (Pl. II., Figs. 3A and B), the sporangium is borne on a very short stalk, and the sporophyll is not specially modified for protective purposes (Text-fig. 4, V.); in the latter species the sporangium has a



Text-fig. 4. II., III., IV. are drawn from sections of typical sporophylls of *Euselago*. II.—(*L. selago*) shews part of an elongated sporophyll, with a mucilage cavity in its base, bearing a very shortly-stalked sporangium. III.—(*L. fontinalis*), shows a very thick short sporophyll, with no mucilage cavity, bearing a sporangium with a slightly longer stalk. IV.—(*L. dichotomum*), is drawn from a very long, thin sporophyll, whose subtending sporangium is furnished with a long stalk. V., VI., drawn from sporophylls of *Subselago*. V.—is from a section of the short sporophyll of *L. squarrosus*, which has a mucilage cavity and bears a sporangium on a very short stalk. VI.—(*L. dalhousianus*), shews a longer-stalked sporangium. Diagonal shading=mucilage cavity.

¹ Bower, 1893, Figs. 8A, 11, etc.

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much longer stalk, and, consequently, although the incurved edges of each sporophyll fold round its sporangium, so that the latter receives a certain amount of protection, it is still distinctly visible between the sporophylls ; (Pl. II., Figs. 4A, B, and Text-fig. 4, VI.) Dehiscence of the sporangium takes place along an apical slit.

A mucilage cavity is present in the base of the sporophyll of *L. squarrosus*. No cells with lignified walls are found in the pedicels of the sporangia of either of these species.

(ii.) *Phlegmaria*. In this group the sporophylls are aggregated to form distinct terminal spikes or cones, and are more or less modified in shape. *L. nummularifolium* and *L. phlegmaria* were examined. The sporophylls of these species (Pl. II., Fig. 6), resemble those of *L. dalhousianum*, but their edges are more closely incurved round the sporangia. Cells with slightly lignified walls are found in the sporangium pedicels (cf. Pl. III., Fig. 2) ; no mucilage cavities are present in the sporophylls. The sporangium of *L. phlegmaria* has an exceptionally long stalk, and dehisces by means of an apical slit.

B. *Rhopalostachya*.

(iii.) *Inundatum*. In the species *L. inundatum*, which by Baker is placed with *L. phlegmaria*, we find for the first time considerable modifications in the structure of the sporophyll, though the external difference between the sporophyll and the vegetative leaf is small.

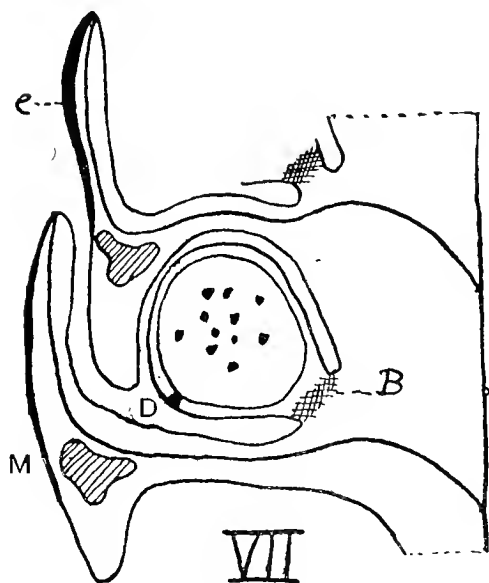
Each sporophyll is of considerable thickness and has a prominent dorsal ridge (Pl. II., Figs. 5A, B). This ridge projects from the back of the sporophyll and overlaps the sporangium belonging to the sporophyll immediately below. The sporangium is thus far less exposed than it is in the *Urostachya*, but it is still visible on the exterior of the cone. A mucilage cavity is found in the ridge (Text-fig. 5, VII.) The sporangium is large and is borne on a very short, wide stalk, in the axil of the sporophyll ; numerous elongated cells with strongly-lignified, pitted walls (Pl. III., Figs. 4, 5), are found in this stalk, but there is no connection between these and the vascular elements of the sporophyll trace. In the tracheides of the trace many interesting examples of a transition from scalariform to reticulate pitting were noticed¹ (Pl. III., Fig. 6).

Pritzel places *L. carolinianum* with *L. inundatum*, and a study of the sporophylls certainly confirms this arrangement². The

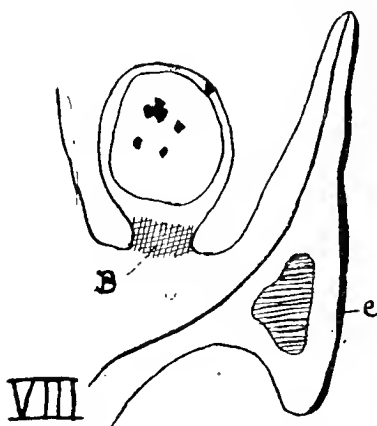
¹ cf. H. Gibson, 1894, Fig. 101, Pl. XII.

² See also Bower, 1908, p. 313.

position of the sporangium is nearly the same in both species, it is not quite in the axil in *L. carolinianum*, but is slightly pushed out on to the sporophyll axis (Text-fig. 6, VIII.); the cells of the very short sporangium-pedicel in *L. carolinianum* have their cell-walls lignified in patches like the similar cells in *L. inundatum*.



Text-fig. 5.



Text-fig. 6.

Text figs. 5 and 6 represent diagrammatic longitudinal sections of sporophylls of *L. inundatum* and *L. carolinianum*. (*m*=mucilage cavity, *b*=lignified cells in sporangium pedicel, *e*=cuticularised epidermis). Each sporophyll has a dorsal flap, and bears a shortly-stalked sporangium, which is axillary in *L. inundatum*, but not quite axillary in *L. carolinianum*.

The dehiscence of the sporangium in both these species is of some interest. It takes place in *L. inundatum* by means of a slit along a line of cells on the ventral surface of the sporangium, on the side furthest from the axis of the cone.¹ In *L. carolinianum* the slit is on the dorsal side, but is slightly displaced laterally. The two flaps of the dehiscid sporangium are thus of unequal size, and the spores are liberated in the most convenient position for dissemination, that is, nearest the opening between the sporophylls. This adaptation is still more strikingly illustrated in some of the more complicated cones.

The systematic position of *L. volubile* is a matter of some difficulty. It is placed by Baker in his sub-genus 4, which includes the other heterophyllous forms, *L. complanatum*, *L. carolinianum*, etc. Pritzel has split up this sub-genus, believing that the common possession of heterophyly is not a valuable systematic character, and while he places *L. carolinianum* with *L. inundatum*, and *L.*

¹ Goebel, Organography II., pp. 582, 583, Fig. 378.

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complanatum with *L. alpinum*, he has connected *L. volubile* with *L. cernuum*. But an investigation of the sporangia and sporophylls by no means supports the last of these suggestions.

L. volubile has a large axillary sporangium, on a stalk of medium length. The sporophyll is perfectly simple, it has no mucilage cavity, and resembles in many respects a sporophyll of *L. dallousianum* or *L. phlegmaria*. In the sporangium pedicel, cells are present whose walls are lignified and pitted like those of the cells in a similar position in *L. inundatum*. As in that species, no connection can be traced between these cells and the vascular elements of the sporophyll trace; in many cases, however, there is continuity between them and the elongated cells with lignified pitted walls which surround the trace and are continuous with similar cells surrounding the stele of the axis. Such continuity is also present in *L. inundatum*, but is not so striking. The line of dehiscence of the sporangium is in a position similar to that in *L. inundatum*, though not displaced quite so far onto the ventral surface.¹

It appears to me that this species occupies a position intermediate between the *phlegmaria* group of the Urostachya and the *inundatum* group of the Rhopalostachya, and it might be to well to place it in a new group (iii.) *Volubile*, at the end of the Urostachya, thus making the *inundata* into group (iv).

Groups (iv.), *Cernua* and (v.), *Clavata*. The species belonging to these two last groups agree in one important point, in which also they differ from all other species. This point is concerned with the position of the sporangium, which here does not arise in the axil of the sporophyll but takes its origin from the sporophyll stalk. An intermediate stage has already been described in *L. carolinianum*. It is found that the sporangium is slightly nearer the axil of the sporophyll in the young cones of *L. clavatum* and *L. cernuum*, than in the adult; (Pl. III., Fig. 7).

In the species of both groups, the sporangium is very efficiently protected, by means of a flap² which grows down from the dorsal surface of the abaxial region of the sporophyll, and thus it is not visible on the exterior of the cone (Pl. II., Fig. 9A). The saddle-shaped appearance of the sporangium is very noticeable in all species. The sporophylls of *Clavata* appear to be less highly modified than those of *Cernua* and I will therefore describe them first.

¹ Engler and Prantl, Teil I., Abt. 3, Fig. 380, E F

² cf. *L. annotinum*, Goebel p 583

(v.) *Clavata*. The protective outgrowth is not well developed in *L. clavatum*, and the stalk of the sporangium of this species is simple in structure, being formed only of short parenchymatous cells which are slightly lignified at the corners (Pl. II., Fig. 7). The sporangium has a very large archesporial pad¹; there is no mucilage cavity in the sporophyll (Text-fig. 7, IX.)

In the sporophylls of *L. alpinum*, the protective flap is better developed (Pl. II., Figs. 8A, B), and the peltate form of the sporophyll is more pronounced. The cells of the sporangium pedicel are elongated and have more strongly lignified walls. The sporophylls of *L. complanatum* are extremely like those of *L. alpinum*. In neither species is there any connection between the lignified cells in the sporangium pedicel and those of the sporophyll bundle.² The sporangium dehisces by a slit which is nearly apical in *L. clavatum* but more displaced onto the abaxial side in the other two species.³

The sporophyll trace of *L. complanatum* differs from that of all the other species examined (Pl. II., Fig. 9). It arises in the usual manner from the axial stele and pursues an obliquely upward course, but this course is continued above the level of the sporophyll base and the trace then bends sharply downwards to enter the sporophyll. This curious behaviour is strikingly similar to that of the sporangium trace in *Calamostachys*⁴ and *Palæostachya*⁵, but it has no analogy among the Lycopods, except perhaps in the trace of *L. clavatum*, which makes a much rounded curve before it enters the sporophyll.

(iv.) *Cernua*. The sporophylls of *L. laterale* (Text-fig. 7, X.) closely resemble those of *L. alpinum*; the lignification in the sporangium stalk is even more strongly pronounced.

The most highly developed cones and sporophylls are those of *L. cernuum*. In this species a groove is present on the under surface of the stalk of each sporophyll, and into this groove (Pl. II., Fig. 9B g.), fits the sporangium borne on the sporophyll immediately below. Obviously, this arrangement, combined with the dorsal flap (f), affords highly efficient protection to the sporangium (see Text-fig. 8, XI.) and

¹ Bower, 1894; p. 518. Note—A similar "pad" was found in an unnamed species which I could not identify but which apparently belonged to the Phlegmaria group.

² Bower noted that in *L. alpinum* there is a slight upward extension of the sporophyll trace towards the sporangium, 1894, p. 522.

³ cf. Engler and Prantl, Teil I., Abt. 3, Fig. 378d.
Renault, 1896, p. 130, Pl. LX., Figs. 3-8.

⁵ Hickling, 1907. Scott, 1907, pp. 159, 165,

a perfectly compact cone is formed, on the outside of which no signs of the sporangia are visible (Pl. II., Fig. 9A). The outer cell-walls of the sporophyll epidermis are provided with a cuticle which is everywhere thickened, but especially on the abaxial surface of the basal part of the dorsal flap¹. Here (e, Text-fig. 8, XI.), it seems to be of use in dragging apart the sporophylls, when they separate to let loose the spores.² The sporangium dehisces by means of a slit, which is placed laterally on the abaxial side, thus liberating the spores in the position most favourable for their dissemination.

There is a large mucilage cavity in the sporophyll stalk, running in a longitudinal direction beneath the vascular bundle.³ The pedicel of the sporangium is made up of short cells whose walls are strongly lignified in transverse bars⁴, (Pl. III., Fig. 7), and present a very striking appearance if stained with Iodine green and Eosin, when they are seen to be made up of alternate patches of pink and green. No connection can be traced between these cells and the vascular elements of the trace which supplies the sporophyll, but only one or at most two layers of cells separates the two tissues.

IV.—CLASSIFICATION.

It appears from the above description that the classification of the genus *Lycopodium* according to Pritzel is in the main supported by a study of the sporophylls of the various species. Throughout the *Urostachya* the sporangium is axillary in position, on a sessile sporophyll; in the higher groups of the *Rhopalostachya* the sporangium takes its origin from the stalk of a peltate sporophyll.

In the *Inundata*, the first group of the *Rhopalostachya*, an intermediate condition is maintained. The sporophylls are stalked and are furnished with a dorsal flap, but the sporangium is axillary in *L. inundatum* and almost axillary in *L. carolinianum*. It does not

¹ cf. Goebel, Organography II., p. 580.

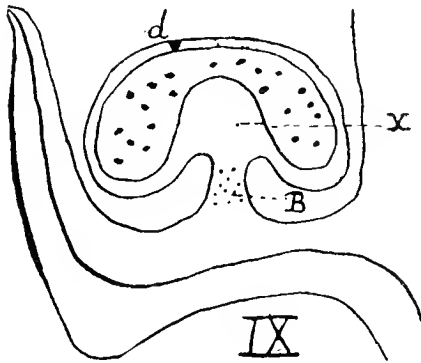
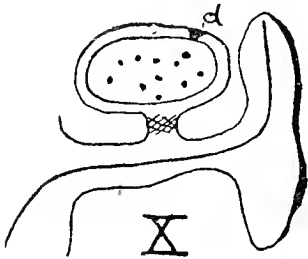
² Experiments have been made on the cones of *L. cernuum*. Cones taken from spirit and herbarium material were soaked water and then were (1) dried in air, or, (2) placed in strong glycerine. In both series of experiments each sporophyll was gradually drawn backwards, at the same time folding its edges together over its dorsal surface, thus exposing the sporangia. Sections were also examined microscopically in strong glycerine. The lignified cells at the base of the sporophyll were seen to gradually contract and an air bubble finally appeared in each cell.

³ cf. T. G. Hill, 1906.

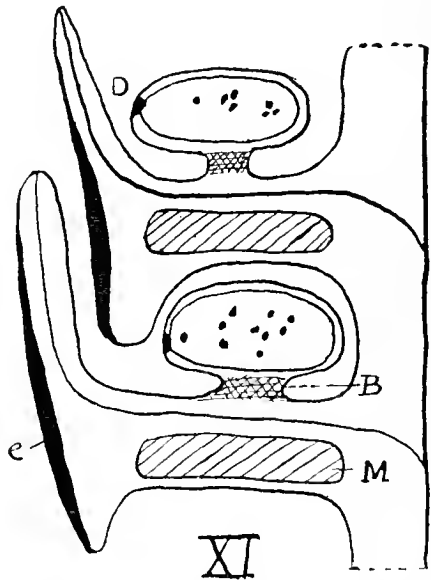
⁴ cf. Transfusion tracheides in Stigmarian rootlets, Weiss, F. E., 1904.

appear certain which of the two great divisions should contain this interesting group, whose half-way position is confirmed by a knowledge of embryology and the gametophyte, and in some ways it would seem more suitably placed in a division by itself. A striking link between it and the *Urostachya* is found in *L. volubile*, whose systematic position has been fully discussed.

In the *Rhopalostachya* it has seemed reasonable, in view of the obviously simpler nature of the *Clavata* to place them before the *Cernua*, but it is not therefore supposed that the two groups are necessarily connected, and indeed, other considerations appear to render it probable that the two groups may represent separate lines of development,¹ both connected with *L. inundatum*.



Text-fig. 7.



Text-fig. 8.

Text-figs. 7 and 8 represent longitudinal sections of species of *Cernua* and *Clavata*, in which groups the sporangium is not axillary but is borne on the stalk of the peltate sporophyll. IX. (*L. clavatum*), shews the large archesporial pad (x) of that species. X. is *L. laterale*. Fig. 8, XI. shews two sporophylls of *L. cernuum*. In each case oblique shading indicates mucilage cavity, and cross-hatching or dots=lignified cells in sporangium pedicel, d=line of dehiscence.

V.—THEORETICAL CONSIDERATIONS.

It has been shown that the sporophylls of the various species of *Lycopodium* can easily be arranged in a series of increasing complexity; considerable difficulty is felt, however, when an attempt is made to decide which end of the series is the more primitive. It

¹ Engler and Prantl, *l.c.*

has been usual to regard the simpler types as primitive, and this view, which is supported by Bower¹ and others, will be considered first.

Theory of Progression.

(a). *Anatomical and Developmental evidence.* Bower regards *L. selago*,² with its elongated, branched strobilus, as the most primitive form of Lycopod, and from such forms he thinks others, with a more restricted spore-producing area, were derived by means of "sterilisation of sporophylls." In *L. Selago*, the distribution of the sporophylls in fertile whorls,³ alternating with sterile ones, and also the presence of abortive sporangia in the axils² of some of the leaves of the sterile whorls, appears to support this theory. Strasburger, writing in 1873,⁴ looked upon the Lycopodian sporangium as a product of the main stem, axial in nature, which has become shifted on to the sporophyll by later growth, but is actually the morphological equivalent of an axillary bud. The relative positions of the sporangia in the young and old stages in *L. selago*,⁵ give support to this hypothesis. Examples of axillary buds in this genus are found in the bulbils of *L. selago* and its near allies, and have been regarded as evidence of the primitive nature of these species.

The position of *Phylloglossum* has been a question of some difficulty. Its simple structure, to which it owed its first name of a "permanently embryonic form of Lycopod,"⁶ is now no longer looked upon as primitive.⁷

Its protocorm and protophylls seem to connect it most closely with the Rhopalostachya, especially with the *Inandata* and *Cernua* from which it seems probable it may have been derived by reduction.⁸ Bower considers now that the protophylls may not be primitive, but are merely a vegetative adaption, and hence he regards them as abortive sporophylls,⁹ but it is extremely difficult to agree with him in this. In *Phylloglossum*, the last of the protophylls is sometimes smaller than the rest and is looked upon as an intermediate stage, while in *L. cernuum* and *L. inundatum* the protophylls are never sharply marked off from the sporophylls.

(b.) *Comparative evidence.* From the simpler Lycopods it is

¹ Bower, 1894 etc.

² Bower, 1901, pp. 246-249 and 1908, p. 711.

³ Bower, 1894.

⁴ Strasburger, 1873.

⁵ Pl. III., Fig. 1.

⁶ Bower, 1885; also 1894, p. 361.

⁷ Bower, 1901.

⁸ Engler and Prantl, Teil I., Abt. 3, p. 582.

⁹ Bower, 1901, p. 228.

fairly easy to derive such a form as *L. inundatum*, and then by increase in complexity to arrive at *L. cernuum*, but on this view it is hard to form an intelligible hypothesis as to the relations of *Lycopodium* with its fossil allies. For, although the external resemblances between *L. cernuum* and *Lepidodendron* suggest a relationship between these two plants, yet if we regard this as the most recent species of *Lycopod*, it can only be nearly related to *Lepidodendron* if that genus be still more recent in origin.

The simpler *Lycopods* are alone in having sessile sporophylls bearing axillary "foliar" sporangia. Bower regards this character as primitive, not only in the genus *Lycopodium*, but in the *Pteridophyta* as a class. But there is little comparative evidence for such a view; indeed recent work has made it almost inconceivable that the genus *Lycopodium* is to be regarded as more primitive than the larger strobiloid *Pteridophytes*.¹

It is almost as difficult to consider this position of the sporangium as primitive in the genus itself. For we must then suppose *Lycopodium* to be derived from some such form as *Spencerites*² by reduction of the sporophyll axis and a consequent simplification of the sporophyll. Then by a shifting of the sporangium and elaboration of the sporophyll the more complex species could be evolved. Here, once more we have a sporophyll which may be aptly compared with that of *Spencerites*, but the comparison is only an analogy, and the petiole of the sporophyll, —the structure found between the cone axis and the point at which the sporangium pedicel takes its origin—is not necessarily of the same morphological nature as the apparently homologous axial structure in the same position in *Spencerites*, *Lepidodendron*, etc. This conclusion may seem somewhat forced, but it appears to me to be the only logical outcome of a belief in the primitive nature of the simple *Lycopods*, if any attempt is made to compare them with fossil genera.

Theory of Reduction.

(a) *Anatomical and Developmental evidence.* A belief in the reduced nature of the simpler types of *Lycopodium* is gradually gaining ground,¹ and would no doubt find still more adherents were it not for the weighty evidence collected by Bower in favour of his "sterilisation theory."

¹ cf. Scott, 1907, p. 175, and Tansley, 1907.

² Berridge, E. M., 1905.

³ cf. Scott, 1907, p. 173.

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L. cernuum is thought by Treub¹ to show a primitive type of embryology, and an examination of the prothalli of various species has also led both Treub and Lang² to look upon this species as primitive. They compare its prothallus first with *L. inundatum* and secondly with that of *Phylloglossum*. It has been shown above³ that an examination of the sporophylls of *L. cernuum* and *L. inundatum* led me to compare the two species, and it also appears to me that the sporophylls of *Phylloglossum*⁴ with their short dorsal outgrowths resemble those of *L. inundatum*. The presence of a protocorm and protophylls in all three forms is necessarily of great interest,⁵ and the absence of these in the simpler types is quite consistent with the theory of the reduced nature of the latter. Bower⁶ states that the embryo of *L. selago* very quickly forms short assimilating leaves, and thus its early nourishment is provided for without any necessity for the formation of an underground protocorm with protophylls. It would seem far more natural to regard the protophyll as an organ useful to the old types with underground prothallia, but lost in the later forms, than as an organ evolved for special purposes from a sterilised sporophyll.

Similarly, notwithstanding Bower's evidence for the origin of all the smaller leaves of a *Lycopodium* from sporophylls by sterilisation, it does not seem absolutely necessary to accept his interpretation of his facts. It is by no means certain that the presence of an arrested organ in any position indicates that a fully-developed organ was ancestrally present in that position.⁸ In other words, if *L. selago* is derived from the more complex types by an extension and simplification of the spore-producing area, we should reasonably expect more primordia to be formed than would become functional.

The study of the development of the sporangium does not throw much light on the question as to which position is the more primitive. The origin rather near the axil of the young sporangia of *L. cernuum*⁹ cannot be regarded as of any great importance since it is easy to see that the later position is brought about by the lengthening of the sporophyll axis. The development of the

¹ Treub; 1884 and 1888.

⁴ p. 42., also Bower, 1908, p. 315.

² Lang, 1899.

⁵ cf. p. 51.

³ p. 50 and p. 52.

⁶ Bower, 1901, p. 249.

⁸ cf. Goebel, I., p. 60. We must "guard against considering all arrested organs as being descended from organs which were developed in the ancestors of existing forms."

⁹ Pl. III., Fig. 7.

sporangium from the main axis in *L. selago* may be merely a contrivance to save time; perhaps the fact that even here it does not appear to be formed from leaf tissues may have some connection with the morphological question as to whether the sporangium is derived from tissues of axial or foliar nature

The series of species constituting the genus *Lycopodium* is far more easily interpreted as a reduction than as an elaboration series.

(I.) For, if the simpler species are primitive, it is difficult to understand the evolution of a stalked sporophyll with a dorsal flap, adapted for the protection of a distally-placed sporangium, whilst bearing its sporangium in an axillary position. Yet such is the state of affairs in *L. inundatum*, and it is easily explicable on the other hypothesis, by which the lax arrangement in *L. selago* arose from a compact cone like that of *L. cernuum* by a series of steps involving the gradual loss of specialised adaptations. For then, we have in *L. inundatum* an intermediate step, in which the dorsal protective flap is still present, but is no longer perfectly effectual, since the sporangium is now not in a distal position on the sporophyll.

(II.) Again the positions of the line of dehiscence in the various sporangia support the second view. A longitudinal section of *L. inundatum*, such as that drawn in Text-fig. 5, VII., shows that the spores are liberated opposite the space between the distal ends of two sporophylls. But the sporangia are not completely enclosed as in *L. cernuum*, and are exposed between the proximal ends of the sporophylls, so that the necessity for this mode of dehiscence is not clear here and is still less obvious in *L. volubile*, where there is not even a dorsal flap to the sporophyll. I think the displacement of the line of dehiscence is best explained in these two species as a reminiscence of the more complex cones in which it was really important, in order to ensure dissemination, to liberate the spores in a lateral position.

(III.) The appearance of the lignified cells at the base of the sporangium in *L. cernuum* so forcibly recalls vascular tissue that one cannot resist the temptation to regard them as primitively vascular in origin. Though of course it is true that the development of vascular tissue cannot be brought forward as evidence of undoubted phylogenetic value, yet these lignified elements are of especial interest in this species, coupled as they are with the existence of a well defined parichnos in the sporophyll. The lignified cells in *L. inundatum*, the walls of which are exactly

similar to those of the elongated elements surrounding the stele in that and other species, may possibly represent another step in the reduction of what may once have been a small vascular bundle while in *L. serratum*, etc., we find an almost complete absence of cells with lignified walls in the sporangium pedicel.

(b.) *Comparative evidence.* If the series of species of *Lycopodium* is a reduction series, a more intelligible hypothesis can be constructed concerning the relations of this genus with recent and fossil Pteridophytes. It is impossible to produce definite evidence as to the direct ancestry of *Lycopodium*. Of the *Lycopodites*,¹ their obvious relations, we know so little that in most cases we cannot ascertain whether any given form is a *Lycopodium* or a *Selaginella*; but there appear to have been no striking differences between this collection of species in the Palæozoic Era and the Lycopodiums of to-day.

It would not be difficult to derive such a plant as *L. cernuum* from *Lepidodendron* or one of its allies. For, even if *Lepidodendron* itself is more nearly allied to *Isoetes*,—as is suggested by the position of the sporangium, and the discovery of a ligule, a parichnos,² and sporangial trabeculæ in both genera—it is still possible to suppose a comparatively close relationship to *Lycopodium*, in the sporophylls of which genus a parichnos is also generally present.³ Perhaps the complex sporophyll present in the *Rhopalostachya* is sufficient for the protection of the young sporangia of such small cones,³ from too great evaporation, and the mucilage once secreted by the ligule⁴ is now no longer necessary. It is conceivable that some such theory may also explain the absence of the ligule in *Spencerites*, which may then be brought into connection with the above genera. It has been already stated that the sporangium in this plant is attached to the stalked sporophyll in a position which is recalled by the tangentially placed sporangium of *Lycopodium cernuum*, etc., while the small lump of tissue or “ventral lobe” found between the sporangium and the distal end of the sporophyll recalls the ligule of *Lepidodendron*⁵; it is possible to regard *Spencerites* as an ancient connecting link between the old *Lepidodendra* and the Lycopodiums,

¹ Goldenburg, 1855; Solms Laubach, 1891, p. 186; Engler and Prantl, Teil I., Abt. 3, p. 715.

² Hill, T. G., 1906; Potonic, '99, p. 239; Weiss, 1907.

³ c.f., Worsdell, 1902.

⁴ Halle, 1907; Gibson, 1896.

⁵ cf. also *Araucariæ*, Seward and Ford, 1906.

perhaps one of the first of a chain of genera which were to form a long reduction series.

Conclusion and Comparison with Conifers. If a series of relationships such as those sketched above could be proved to have existed, I should be inclined to regard the stalk of the "sporophyll" in *Lepidodendron*, *Spencerites* and *L. cernuum*, etc., as axial in nature,—comparable in all species with the similar structure in *Calamostachys*, *Palaeostachya*, *Psilotaceæ* and *Sphenophyllum*¹—and representing the axis of a branch, terminated by a single sporangium in the one series, by several sporangia in the other series, and bearing also a single leaf with which its association is probably secondary, not primitive.² In the simpler Lycopods this axis has become reduced and has then finally disappeared; but even here the young sporangium is not developed from the actual substance of the leaf rudiment, but from the cone axis, and hence arises in the position of an axillary bud. Rudiments, at first exactly similar in appearance to the sporangial rudiments, often give rise to axillary bulbils. These may be looked upon as due to the proliferation of the apex of the reduced axis, which is usually terminated by the sporangium.³ Such proliferation is not necessarily a primitive character, but may be traced to purely mechanical causes,—for instance, a bud developed from as small a mass of tissue as that found in the sporangium stalk of *L. cernuum*, etc., is necessarily itself small, and may well only produce a sporangium, but a bud arising from the axis of the cone has more material to draw upon, and can thus form stem and leaves.

It appears that the sum of evidence available is in favour of the hypothesis that the simpler Lycopods are reduced, not primitive, and that the whole genus *Lycopodium* contains a series of types which are reduced from the larger strobiloid Pteridophytes. The foliar position of the sporangium is looked upon as secondary, and the Lycopodian sporangium-bearing organ is here supposed to have been derived from a branch structure, which had the morphological value of an axillary bud.

Whilst our knowledge is still so uncertain, it is impossible to attempt any satisfactory comparison between the sporophylls of the Lycopodiales and those of Conifers. The female flower of *Taxus*, apparently terminal, but shown by Celakovsky (1879) to be

¹ cf. Sykes, M. G., 1908, pp. 80-83. Text-fig. A.

² Ibid, p. 82.

³ cf. Thomas, 1901, abnormalities in *Tmesipteris* sporophylls.

Sporangium-bearing Organs of the Lycopodiaceae. 57

really axillary, is of course a proliferated axillary bud, and it is perhaps interesting to compare it with a bulbil of *L. selago*, though such analogies cannot have any morphological value.

VI.—SUMMARY OF RESULTS.

I. The sporophylls of the different species of *Lycopodium* can be arranged in a continuous series, increasing in complexity of structure. In the simplest forms, such as *L. selago*, the sporangium is almost completely exposed, whilst in *L. cernuum*, the most highly differentiated species, the sporophyll has a dorsal flap, and affords perfect protection to the sporangium.

II. In *L. cernuum*, and nearly allied species, the adult sporangium arises from the sporophyll stalk; but in all the simple forms it is found in the axil of the sessile sporophyll. In intermediate cases, such as *L. inundatum* and *L. carolinianum*, the sporophyll is stalked, but the sporangium is axillary. Even in *L. selago*, however, the young sporangium is not differentiated from leaf-tissue, but is formed from the axis of the cone itself.

III. No definite vascular bundle supplies the sporangium pedicel, but in it are often found elongated cells with more or less lignified walls. These are very simple in some species (*L. serratum*, *Phylloglossum*, etc.), very highly specialised in others (*L. volubile*, *L. inundatum*, *L. cernuum*, etc.), but they are never directly connected with the sporophyll trace, though in *L. volubile* they were found to be in continuity with the layer of cells with lignified walls which surrounds the trace.

IV. Our present knowledge of the relations of the Lycopods, both amongst themselves and with fossil genera, appears to be insufficient to determine certainly which way we shall read the above series, that is, whether we consider the simpler Lycopods to be primitive or reduced. Evidence, based on embryology and the structure of the gametophyte, tends to support the latter view; it is also easier to find connections between the more complex members of the series and fossil genera. The series itself is far more naturally regarded as a reduction series, and the intermediate forms are then far more easily explained. The sporophylls of *Phylloglossum* are found to be comparable with those of some of the intermediate species, and it seems probable that this genus represents a reduced form, as has been recently decided by Bower.

V. From anatomical, developmental, and comparative evidence, it is concluded that the genus *Lycopodium* is to be regarded as reduced from some of the larger strobiloid Pteridophytes, and that the genus itself is also composed of forms which can be arranged in a reduction series and the evolution of which is still traceable among the species alive to-day.

VI. If it be granted that the "sporophyll" of *L. cernuum* shows the more primitive arrangement, it would seem to me to be natural to regard it as an axial structure, morphologically equivalent to a reduced branch, which is terminated by a single sporangium, and bears also a single leaf, with which, however, its association need not necessarily be primitive. A similar interpretation has before been given to the sporophylls of some of the allied fossil and recent Pteridophytes.

The work for this paper was begun at the Botany School, Cambridge, while holding a Bathurst Studentship at Girton College, and was continued in the Botanical Laboratory of the Royal Holloway College.

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EXPLANATION OF PLATES II. AND III.

ILLUSTRATING MISS SYKES' PAPER ON LYCOPODIACEÆ.

PLATE II.

All the figures except 1A, 3A, and 4A, were drawn from preparations examined with the aid of a binocular microscope for the study of solid objects.

Fig. 1A. Apical region of a plant of *L. selago*, shewing numerous fertile leaves bearing sporangia ; (natural size).

Fig. 1B., front, and Fig. 1C, side, views of sporophylls of *L. selago*.

Fig. 2. Sporophyll of *L. serratum* ; (drawn in reversed position).

Fig. 3A. Portion of fertile region of *L. squarrosnm* ; (natural size).

Fig. 3B. Sporophyll of ditto.

Fig. 4A. Apical portion of fertile region of *L. dalhousianum* ; (natural size).
The sporangia are to some extent hidden by the sporophylls.

Fig. 4B. Sporophyll of ditto, showing incurved edges.

Figs. 5A. & B. Side and back view of sporophyll of *L. inundatum*. r = dorsal ridge.

Fig. 6. Sporophyll of *L. phlegmaria*, showing incurved edges.

Fig. 7. Sporophyll of *L. clavatum* with small dorsal flap.

Figs. 8A & B. Front and side views of peltate sporophyll of *L. alpinum*.

Fig. 9A. Cone of *L. cernuum* (natural size). The sporangia are entirely hidden by the sporophylls.

Figs. 9B & C. Sporophyll of *L. cernuum*. ; f = downward flap ; g = groove in stalk of sporophyll into which fits the sporangium borne by the sporophyll next below. The mucilage cavity present in the stalk gives it a transparent appearance.

PLATE III.

Fig. 1. Longitudinal section of the apical region of the stem of *L. selago*, showing origin of (sp) sporangial, and (lf) sporophyll rudiments. × 78.

Fig. 2. Longitudinal section of the stalk of a sporangium of *L. serratum*, shewing typical elongated cells with their walls lignified at the corners. × 116.

Fig. 3. Longitudinal section of axis of *L. selago*, comprising the area between two sporophyll traces. The inner and outer cortex are composed of more or less compact cells while the middle cortex is made up of very lacunar tissue. A few layers of compact cells surround the sporophyll trace and accompany it through the middle cortex. × 116.

Fig. 4. Longitudinal section of part of a sporophyll of *L. inundatum* showing cells with lignified walls in the sporangium pedicel ; a = axis of cone ; sp = stalk of sporophyll with trace ; ep = epidermis of sporangium with strongly lignified bars ; m.c. = mucilage cavity. × 78.

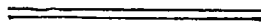
Fig. 5. Two cells from the pedicel in Fig 4. × 400.

Fig. 6. Part of a tracheide from the sporophyll trace in Fig. 4, showing a transition from a scalariform to a reticulate form of pitting. × 400.

Fig. 7. Longitudinal section of very young sporophyll of *L. cernuum* showing young sporangium, in a position nearer the axil than in the adult cone ; letters as above. × 116.

Fig. 8. Longitudinal section of part of adult sporophyll of *L. cernuum* ; st = sporangium pedicel, which is composed of cells whose walls are strongly lignified in bars. × 116.

Fig. 9. Longitudinal section of base of sporophyll of *L. complanatum*, showing the course of the sporophyll trace ; (see text). × 78.



SKETCHES OF VEGETATION AT HOME AND ABROAD.

IV.—WICKEN FEN.

BY R. H. YAPP, M.A.,

[PLATE IV. AND TEXT-FIGS. 9-15.]

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INTRODUCTORY.

THE following sketch has been written, partly on account of the general interest which centres in the vegetation of the now, for the most part, drained "Fenland"; and partly as an introduction to more detailed studies, dealing with certain problems connected with marsh vegetation. As the work has been hitherto carried out chiefly at Wicken Fen,¹ the present preliminary sketch will deal mainly with this limited part of the Fen area.

The Fens of the East of England form a great plain, the largest in Britain, comprising some 1,300 square miles of practically level country. In reality the Fenland is a complex delta, formed by what are now the Witham, the Welland, the Nene and the Great Ouse; just as a large portion of the Western Netherlands, on the other side of the North Sea, has been formed as the delta of the Rhine, the Maas and the Scheld.

According to Skertchly, the Wash was once a great bay—co-extensive with the Fenland itself²—which occupied a basin hollowed out in the Jurassic clays.³ It would seem improbable, however, that the Wash ever extended quite to the southern part of the area, where the deposits consist almost exclusively of pure peat⁴ (cf. Text-fig. 9).

This great shallow bay has been gradually silting up since post-glacial times.⁵ The silted up portion has formed the northern Fens, whilst the present Wash, the shrunken remnant of the bay, is still becoming smaller year by year, through the continuance of the silting process. The floor of the Fenland basin "is probably not a very even surface, but silt deposited by the sea, mud brought down by the rivers, and vegetation growing upon the surface have built

¹ By the kind permission of G. H. Verrall, Esq.

² Miller & Skertchly, *The Fenland*, Wisbech, 1878, p. 224.

³ *Ibid.* p. 497.

⁴ Reed, *Geology of Cambridgeshire*, 1897, p. 222, says, "The southern limit of the silt marks the shore of the great bay—the predecessor of the Wash: but owing to the frequent invasions of the sea into the flat peat-country this line is complicated and indefinite."

⁵ Miller & Skertchly, *l.c.* p. 575.

up the area to a very uniform plain not more than a foot or two above mean-tide level.”¹

The Fen-deposits consist largely of peat and silt. The former is developed chiefly in the south, but is also found along the western boundary of the area—*i.e.*, in those parts most remote from the sea—while the latter is the chief deposit found bordering on the Wash (Text-fig. 9). Boulder clay is often found underlying both peat and silt, which proves the post-glacial origin of the Fen-deposits proper.²

During pre-Roman times the Fens had become for the most part a great swampy plain, probably studded with shallow open meres, similar to the Broads of Norfolk and Suffolk. Here and there, especially towards the south, extensive drier areas, the “Fen islands,” appeared wherever the land was raised a few feet above the general level.

But although the thickness of the peat,³ or turf as it is called by the Fenmen,⁴ attests the long continuance of swamp conditions, yet these conditions did not remain altogether uniform. Proof of the variation of physical conditions is afforded by the alternating beds of silt and peat to be found in the northern part of the Fen area⁵; and also by the buried forests, which indicate a recurrence of drier conditions, found in the peat of certain of the more southern parts of the district. These variations are usually attributed to slight oscillations of level,⁶ but the cause of the oscillations appears uncertain. Probably earth-movement played some part, but other factors may also have contributed their share in bringing about these changes. Such are on the one hand, the blocking of river mouths by sand-banks or silt-deposits, with the consequent damming back of the river water, and on the other, the subsequent breaking through of such barriers. The raising of the general level by the upward growth of the peat, would also assist in the local production of drier conditions.

¹ Marr & Fearnside, *The Physiography of Cambridgeshire* (in *The Natural History of Cambridgeshire*, edit. by Marr and Shipley, 1904), p. 5.

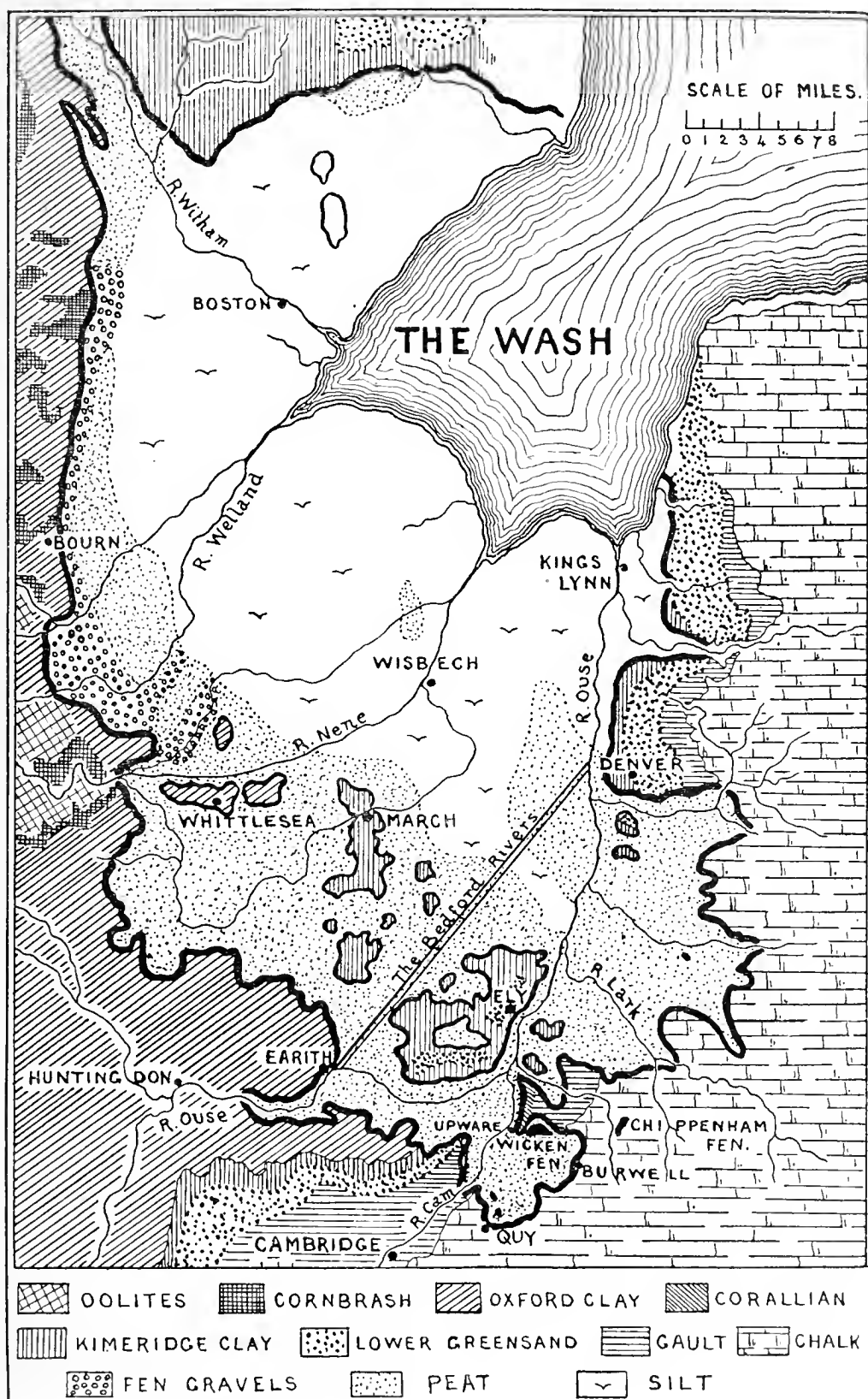
² Miller & Skertchly, *l.c.*, p. 497.

³ A thickness of eighteen feet has been measured at Earith, but the average thickness is much less, Reed, *l.c.*, p. 225. The peat is still used as fuel in some parts of the Fens: cf. the photograph showing peat cuttings on Adventurers' Fen (Plate IV., Fig. 3).

⁴ As in Ireland and elsewhere, cf. German *Torf* and French *tourbe*.

⁵ Miller & Skertchly, *l.c.*, p. 560.

⁶ *Ibid*, p. 561.



Text-fig. 9.—MAP OF THE FENLAND.

The boundary of the Fen area is shown by the black thick line. The "Fen islands," found chiefly rising out of the peaty lands to the south, are also outlined in black. Note the positions of some of the still undrained spots (black) *e.g.*, Wicken, Chippenham (really a valley Fen, outside the Fenland proper), Quy, &c., Adventurers' Fen (see Pl. IV., Fig. 3), which is partly drained, lies immediately to the south of Wicken Fen.

According to Skertchly,¹ no fewer than five forest periods intervened during the deposition of the peat.² These Fen forests consisted of oak, elm, birch, Scotch fir, yew, hazel, alder and willows: of these the oaks formed about eighty per cent.³ The forests never extended over the whole of the Fenland, nor did they cover even that part where peat has been deposited. "They are found almost everywhere around the Fens, wherever peat exists, but never run more than a few miles out into the Fens, with the exception of the willows and salallows, which are ubiquitous."⁴ The peat forests then would seem to have formed mere fringes to the drier uplands; the trees from the latter extending on to the peat whenever it became dry enough to support them. Any subsequent slight depression of the land-surface, or raising of the water-level, would cause the destruction of the fringing forests, and usher in a new local period of swamp conditions.

But the artificial drainage of the Fens⁵ has changed their whole aspect, and the once luxuriant growths of marsh plants have been, for the most part, reduced to insignificant fringes around the drains or "lodes" which intersect the country in every direction. Only in a few favoured spots, of which the chief is Wicken Fen, do these remnants of an extensive flora still form a conspicuous feature of the landscape.⁶

WICKEN FEN.

Wicken Sedge Fen, which together with Wicken Poors' Fen⁷ and St. Edmund's Fen forms an area of nearly 400 acres, lies at almost the extreme S.E. corner of the Fenland. It is bounded on the west, north and east by the higher lands of the "Upware

¹ *Ibid.* p. 566, cf. also the diagram facing p. 304.

² Cf. the succession of buried forests in peat in Scotland, Ireland, Denmark and Norway.

³ Miller & Skertchly, *l.c.*, p. 567. A particularly fine oak was unearthed a few years ago, and is still to be seen, in Adventurers' Fen (see Pl. IV., Fig. 3), a few hundred yards to the south of Wicken Lode. The part of the trunk which still remains is more than sixty feet long.

⁴ Miller & Skertchly, *l.c.*, p. 568.

⁵ Cf. Miller & Skertchly, *l.c.*, Chap. VI., and also the many other accounts of the draining of the Fenland.

⁶ An excellent short account of the Fen flora has been given by Wallis, *The Flora of the Cambridge District* (in the *Nat. Hist. of Cambridgeshire*), pp. 217, *et seq.* The positions of some of these still undrained Fens are shown in the map forming Text-fig. 9.

⁷ On the third Monday in July the poor of Wicken village are entitled to cut as much sedge, &c., on this part of the Fen as they can. But each man must work unaided: no one can employ others to help him in the cutting.

Ridge" and outcrops of Cretaceous rocks, but is open to the south, where it was formerly continuous with Adventurers' Fen, Burwell Fen, &c., see Text-fig. 9.

Although lodes and drains bound the Fen, and also intersect it in various directions, Wicken Fen is still practically undrained, as it is only the surplus rain-water which finds its way *via* Reach Lode into the River Cam. There is no artificial pumping of water from the system of lodes with which the Fen is connected. It seems to be therefore generally supposed that Wicken Fen is still in a primitive condition.¹ But when we speak of "primitive conditions," it must be remembered that Wicken is one of those areas which, fringing the more permanent dry land, have alternated in past times between the two extremes of swamp and forest, with of course all kinds of intermediate stages. It is indeed probable that at all times the vegetation, like the physical conditions which have influenced it, has been in a gradual but continuous state of change.

But whatever its exact past history may have been, Wicken Fen at the present time exhibits all the features of a drying-up marsh; in fact, as will be seen below, it may almost be said to be verging on another forest period.

GENERAL ASPECT OF THE FEN.

Wicken Fen itself "appears during most seasons of the year as a brown waste dotted with bushes" ² (see Pl. IV., Fig. 1). In the winter, as but few of the plants are evergreen, practically the whole Fen acquires the nearly uniform dull brown of the dead vegetation. If visited in May, however, the vivid greens of the newly foliated bushes, rising above the herbaceous vegetation, afford a pleasing contrast to the sober browns of the sedges and grasses. As the summer wears on, the contrasts are subdued, for while the leaves of the bushes darken, the mass of the vegetation assumes a distinctly greenish tinge. But even now the general effect is brown rather than green, for the reason that the dominant plants are grass-like Monocotyledones, the leaves of many of which have the curious habit of early dying off at the tip, while the rest of the leaf remains green and functional. Before the sombre hues of winter are reached again, the prevailing browns may be relieved in autumn by the gold of the withering reeds, and the splashes of red where fruiting bushes of *Viburnum*, &c., rise above the dying sedge.

¹ C. Kingsley. *The Fens*, in *Prose Idylls*, p. 91 (1889 edition), also Marr and Fearnside, *l.c.*, p. 6.

² Wallis, *l.c.*, p. 220.

CHARACTER OF THE VEGETATION.

Two of the most important "plant formations" which give rise to peat deposits are those known to British plant-geographers as Marsh and Bog.¹ These correspond respectively to the *Sumpfmoor* and *Sphagnummoor* of Warming,² and to the *Flachmoor* and *Hochmoor* of Früh and Schröter.³ According to the latter authors, both types may be developed either directly on merely boggy soil, or else on the surface formed by the growing up of open sheets of water by aquatic and semi-aquatic plants.⁴ Thus in many cases the marsh or "Flachmoor" may directly succeed the reed-swamp.

Marsh vegetation is developed where the water is rich in mineral food substances, especially lime: or in running water even if poor in salts. Bogs on the other hand are only formed where the water is deficient in salts, and especially in lime. Another important factor is climate. Bogs can develop fully only in regions with a considerable rainfall, while marsh vegetation is more independent of the amount of precipitation, provided there is a sufficient supply of telluric water.⁵

The Fenland, with its relatively low annual rainfall,⁶ and with some of its streams directly draining the Chalk⁷ or other calcareous strata (see Text-fig. 9), is, like the region of the Norfolk Broads, suited to the development of marsh rather than bog vegetation.

The vegetation of Wicken Fen is then, for the most part, that of a typical marsh or "Flachmoor." The characteristic plants of the bog—*Sphagnum*, *Eriophorum*, *Ericaceæ*, &c., are absent; but instead of these the dominant plants are grass-like Monocotyledones—*Cyperaceæ*, *Gramineæ* and *Juncaceæ*, which give the general facies to the vegetation. Mixed with these are many Dicotyledonous herbs, the whole forming, in most places, a dense rank vegetation some two to five feet in height (see Plate IV., fig. 1).

¹ R. & W. G. Smith. Botanical Survey of Scotland, III. and IV. Forfar and Fife. Scot. Geog. Mag. Vol. XXI., 1905, pp. 117, *et seq.*

² Warming. Oekologischen Pflanzengeographie, 1896, p. 171.

³ Früh & Schröter. Die Moore der Schweiz, 1904, pp. 11, *et seq.*

⁴ *Ibid.*, pp. 12 and 13.

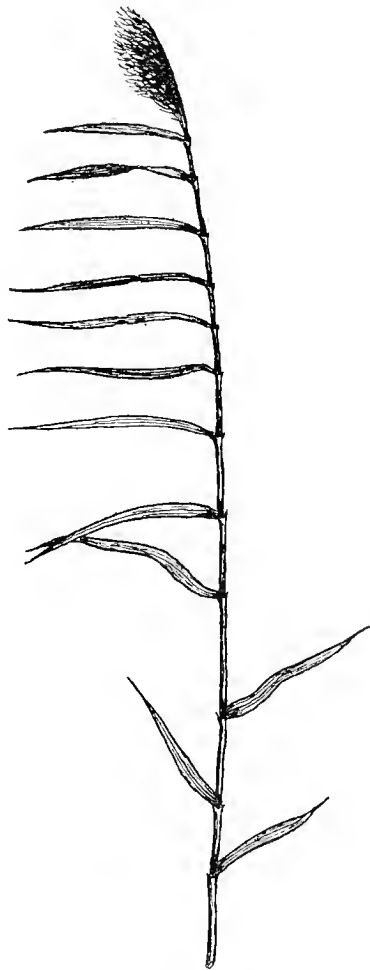
⁵ Transitions between the vegetation of marshes and bogs are often to be found, cf. Smith, *l.c.*, p. 117.

⁶ Miller and Skertchly, *l.c.*, p. 239.

⁷ The presence of calcium in the water and peat of Wicken Fen is proved by the abundance of lime-encrusted Charas in the lodes, and by the great numbers of molluscan shells which are found everywhere in the peat.

So compact is this herbage, that the seedlings and small plants forming the lowest layer, frequently show all the characteristics of plants grown in deep shade.

Fringing many of the lodes, which contain a number of aquatic species, are narrow reed-swamps, with *Phragmites communis* as the dominant species (cf. Text-fig. 11). *Scirpus lacustris*, *Alisma Plantago*, &c., are fairly abundant, while *Butomus umbellatus* (Plate IV., fig. 2) and other species are occasionally met with. Landwards the reeds are largely replaced by Carices, &c., as the reed-swamp passes into the drier marsh (Text-fig. 11). Warming calls attention to the readiness with which the tall slender leaves or un-branched shoots, so characteristic of reed-swamp plants (cf. Plate IV., fig. 2), will yield to the action of wind and water, and the elasticity with which they recover themselves.¹ In this connection the behaviour of *Phragmites*, when exposed to strong winds, may be mentioned. The habit of this plant, with its tall stem and numerous rather broad leaves is well known. Now the inner part of the long leaf-sheaths is smooth and polished (as is also the case in some other grasses). This enables the leaves, when exposed to a strong wind, to readily twist round to the lee side of the stem, and thus to stream out in the direction of the wind, instead of opposing themselves to its violence (Text-fig. 10). The leaves, as may be seen in the sheltered lower part of the stem, are really inserted according to the usual $\frac{1}{2}$ -phyllotaxy.



Text-fig. 10.
Phragmites communis, showing effect of wind. The lower leaves are sheltered, and retain their normal position.
(August).² $\times \frac{1}{15}$.

At the margins of the lodes, the process of land-formation, by the growth of either reeds or other large plants, or of "Schwing-rasen," may be everywhere seen in miniature. But both reed-swamps and the early stages of land-formation can be seen on a

¹ Warming, *l.c.*, p. 163.

² The Text-figures are from sketches made in the field. The month in brackets after the description of each, shows the time of the year when the sketch was made.

far larger scale in the Norfolk Broads.¹ The general vegetation of Wicken Fen, however, affords an excellent example of some of the more advanced stages in the formation of dry land from marshes; and it is with this vegetation that the remainder of the present sketch will deal.

The dominant herbaceous plants are *Cladium Mariscus*, *Molinia coerulea* and *Phragmites communis*, though *Juncus obtusiflorus* and several species of *Carex* are exceedingly abundant. But though here and there either *Cladium* or *Molinia* or even *Phragmites* may be locally dominant, almost to the exclusion of the other two, so that we might speak of "Molinietum," &c., associations; yet, for the most part, the vegetation presents a bewildering tangle of the most mixed character. The dominant species are present in almost every conceivable proportion, while intermingled with them are ever varying numbers of other constituents of the vegetation: so that a definite mapping of the different plant associations represented here would be a difficult, if not an impossible task. To some extent this intermixture is probably due to the periodic harvesting of the vegetation. The latter is classified by the Fenmen into "sedge" and "litter." The "sedge" is the vegetation where *Cladium* is dominant: this is harvested about once in four years, and is mainly used for thatching. "Litter" on the other hand is the name applied to the more mixed vegetation, which is cut about once in two years, and is used as litter, or even in some cases as fodder for farm stock. Now *Cladium* is a slow-growing evergreen plant, which will form, if left to itself under favourable conditions, very dense growths, often to the exclusion of other species. The periodic cutting almost undoubtedly leads to a greater admixture with it of more rapidly growing plants, while excessive cutting may even result in its local extermination. But other changes in the vegetation, which cannot be so readily attributed to the cutting, seem to have taken place in recent times. These will be dealt with later in this paper.

RELATIONS OF THE PLANTS TO SOIL MOISTURE.

Wallis² gives two lists, which contain a few of the more important species found respectively in the dry and damp portions

¹ Stalham Broad for instance, close to which is situated Mr. Gurney's Sutton Broad Laboratory, shows very finely many of the earlier stages in the formation of land from an open sheet of water, through the agency of swamp and marsh vegetation.

² Wallis, *l.c.*, p. 220.

of the Fen. But in reality one finds on Wicken Fen all kinds of plants intermediate between on the one hand, those that live submerged in water, and on the other hand, mere aliens which have migrated from the surrounding dry lands to the drier parts of the Fen soil. The following list (the result of many observations in the Fen district and elsewhere) is an attempt to place some of the commoner marsh plants approximately in order, with respect to the degree of soil moisture which would seem to be the optimum. It must be remembered however, that such a list can be at best only a tentative one, as each species will possess a wider or narrower range of possibilities as to the moisture conditions to which it can adapt itself. For instance, *Hydrocotyle vulgaris* and *Polygonum amphibium* possess a very wide moisture range, while many submerged aquatics, e.g., *Potamogeton lucens*, have but a narrow one. Further, this list refers to the conditions in respect to soil moisture only. The effect, scarcely less important, of varying atmospheric moisture will be dealt with in a future paper.

The list¹ then represents the average relative positions, with respect to soil moisture, in which, so far as my experience goes, it is most usual to find the subterranean parts (roots, rhizomes, &c.), of some of the characteristic Fen plants.

A. AQUATICS.

- 1.—*Chara*, *Nitella*, &c.—whole plant submerged.
- 2.—*Myriophyllum*, *Potamogeton*, *Hottonia*, &c.—vegetative parts submerged, flowering shoots above water.²
- 3.—*Nymphaea*, *Sparganium natans*, &c.—leaves floating.

B. SEMI-AQUATICS.

- 4.—*Sagittaria*,—submerged and aerial leaves.
- 5.—*Scirpus lacustris*,—submerged leaves and tall green aerial stems.
- 6.—*Bontonus umbellatus*, *Sparganium erectum*, *Alisma Plantago*, (*Polygonum amphibium*)—aerial leaves.

C. WET-MARSH PLANTS.

- 7.—*Phragmites communis*.
- 8.—*Juncus obtusiflorus*, *Cladium Mariscus*.¹
- 9.—Many of the Carices, *Orchis incarnata*, *Caltha palustris*, *Menyanthes trifoliata*.

¹ The names used in this paper are those given in Britten and Rendle's *List of British Seed-plants and Ferns*. London, 1907.

² Sometimes even the flowering shoots may be submerged, e.g., last May I found some specimens of *Hottonia palustris* submerged in rather deep water. Many of the flowers had fully opened under water, but were much smaller than the normal ones.

D. INTERMEDIATE FORMS.

- 10.—*Lastrea Thelypteris*, *Iris Pseudacorus*, *Thalictrum flavum*, *Lathyrus palustris*, *Lythrum Salicaria*, *Oenanthe Lachenalii*, *Hydrocotyle vulgaris*, *Lysimachia vulgaris*, *Mentha aquatica*, *Galium palustre*, &c.
- 11.—*Ophioglossum vulgatum*, *Calamagrostis epigejos*, *Agrostis canina*, *Potentilla sylvestris*, *Angelica sylvestris*, *Valeriana dioica*, *V. officinalis*, *Scabiosa Succisa*, *Carduus pratensis*, &c.

E. DRY-MARSH PLANTS.

- 12.—*Molinia coerulea*, *Aira caespitosa*, *Pencedanum palustre*, *Convolvulus sepium*.²
- 13.—*Spiraea Ulmaria*, *Symphytum officinale*, *Eupatorium cannabinum*.

F. ALIENS FROM THE DRY LAND.

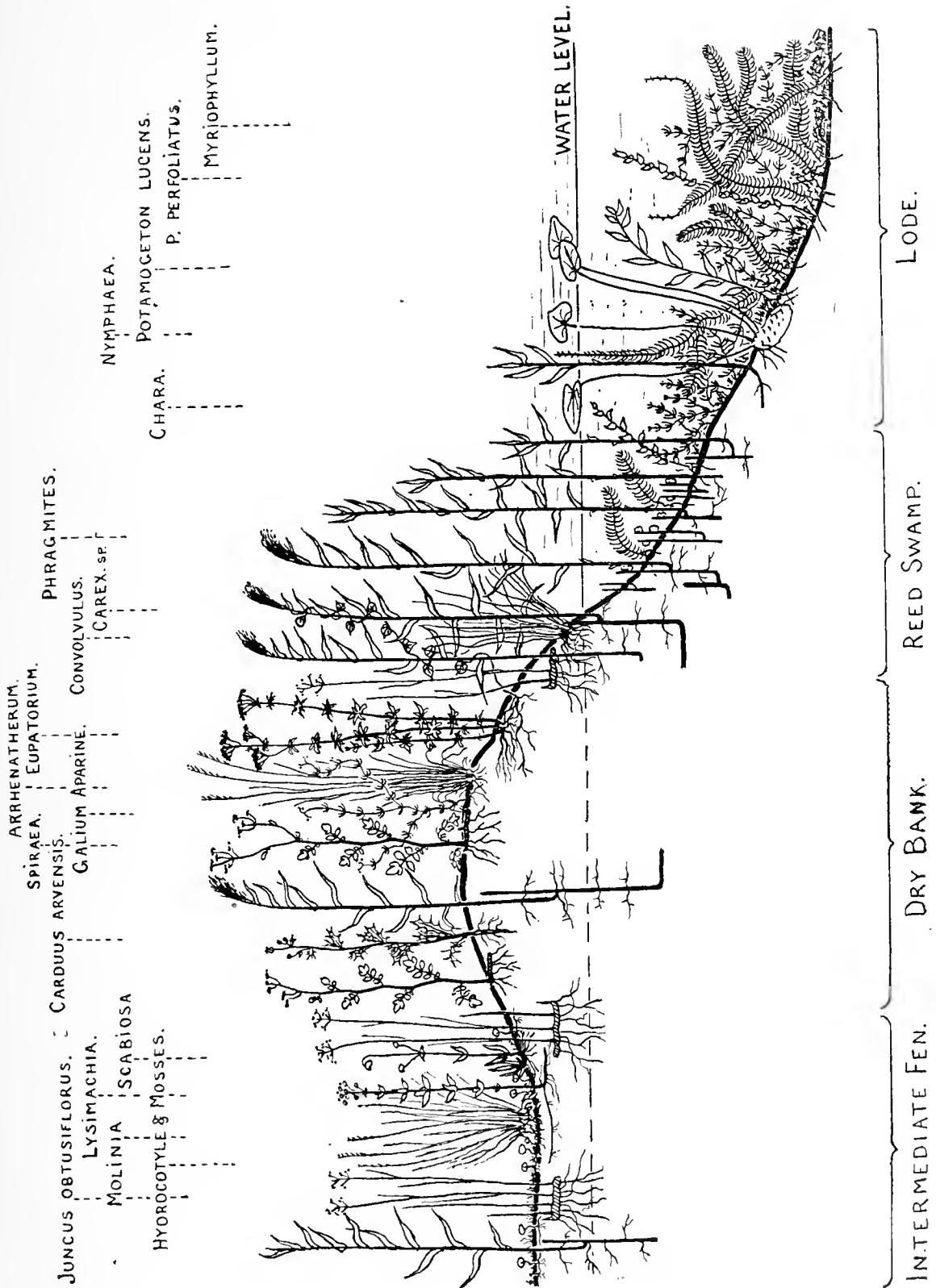
- 14.—*Arrhenatherum elatius*, *Urtica dioica*, *Ajuga reptans*, *Galium Aparine*, *Centaurea nigra*, *Carduus arvensis* and many others.

The plants included in the above list are a heterogeneous assemblage of forms, of very varied habits, which grow under a variety of conditions. Broadly speaking, the majority of the semi-aquatic and wet-marsh plants are Monocotyledones, whilst the Dicotyledones become increasingly important towards the dry end of the series. Some of the latter are by no means confined to even dry marshes, but are commonly found by river banks, or in moist pastures, or in hedgerows bordering on damp ditches. Such are *Spiraea Ulmaria*, &c. But all the plants, except the aliens, are species usually found on soils with a moisture content above the average.

The ground surface of Wicken Fen, although fairly flat in a general way, has many slight inequalities. In some parts there are gentle parallel undulations, which possibly mark the positions of former peat diggings, and there are many smaller elevations and depressions. Moreover, in excavating the Fen lodes, the dug-out peat was deposited so as to form banks raised a foot or two above the general level (see Text-fig. 11).

Though no artificial pumping is resorted to, the surplus water soon drains off, by means of the lodes, into the River Cam; with

¹ and ² It will be seen that *Cladium* and *Convolvulus* are assigned to different places in this list to those in which they were placed by Wallis (*l.c.*, p. 220). It is true that *Cladium* is often found in places where the surface soil is firm and fairly dry, while *Convolvulus* is found binding the stems of *Phragmites* together. But the roots of the former are found in very wet soil, or even in water, while those of the latter grow in drier soil.



Text-fig. 11. Section showing relations of some Fen plants to soil moisture. It passes from Wicken Lode, through its fringing reed-swamp and the dry bank, to a part of the Fen with intermediate moisture conditions. Scale, about $\frac{3}{10}$ " to a foot (September).

the result that the general water level is fairly constant. Except after heavy rains it rarely varies, in all probability, either in winter or summer, more than some three to six inches. Only when the Cam itself is in flood, and rises above the level of the apertures in the Upware sluices, is there any danger of the Sedge Fen being inundated. At most times of the year the soil is firm, and one can walk dryshod over the greater part of the Fen. Apart from the more marked elevations and depressions, the actual water level is found, say in the summer time, at depths varying on different parts of the Fen, from some four inches to about a foot below the surface. But as a rule the water-content, even at the surface, is high, owing to the great water capacity of peat.¹

These differences of level, by affecting the amount of soil moisture, exert a profound influence on the distribution of the Fen plants. For instance, at certain times of the year it is perfectly easy to pick out, even from a distance, all those parts of the Fen which are raised above the surrounding level, by means of the plants growing on them. Thus towards the end of July, many of the banks and raised patches dotted about the Fen, are easily recognised by the masses of flowering *Spiraea Ulmaria*, which at the present time is exceedingly abundant at Wicken. Where the Fen in general is comparatively dry, the patches are less distinct, but where they are raised above a fairly wet part, these *Spiraea* "islands" are sharply defined. Associated with *Spiraea* on the "islands" are frequently *Eupatorium cannabinum* (which flowers later than *Spiraea*) and *Symphytum officinale*; sometimes also *Convolvulus sepium*, *Agrostis canina*, &c., and, if the soil is dry enough, a few aliens such as *Urtica dioica*, *Centaurea nigra*, &c.

But as Wallis points out,² the "wet plants" frequently invade the dry places, while the "dry plants" are not so usually found encroaching on the wetter parts. Thus *Phragmites* (or occasionally *Juncus obtusiflorus*) may often be found on a *Spiraea* "island," and indeed commonly occurs on the drier banks of the lodes (Text-fig. 11). This is no doubt due in large measure to the habits of growth of the subterranean parts of these plants.

It is a well known fact that the underground parts of marsh plants are much more extensively developed than those of bog plants.³ Creeping subterranean stolons and rhizomes are very

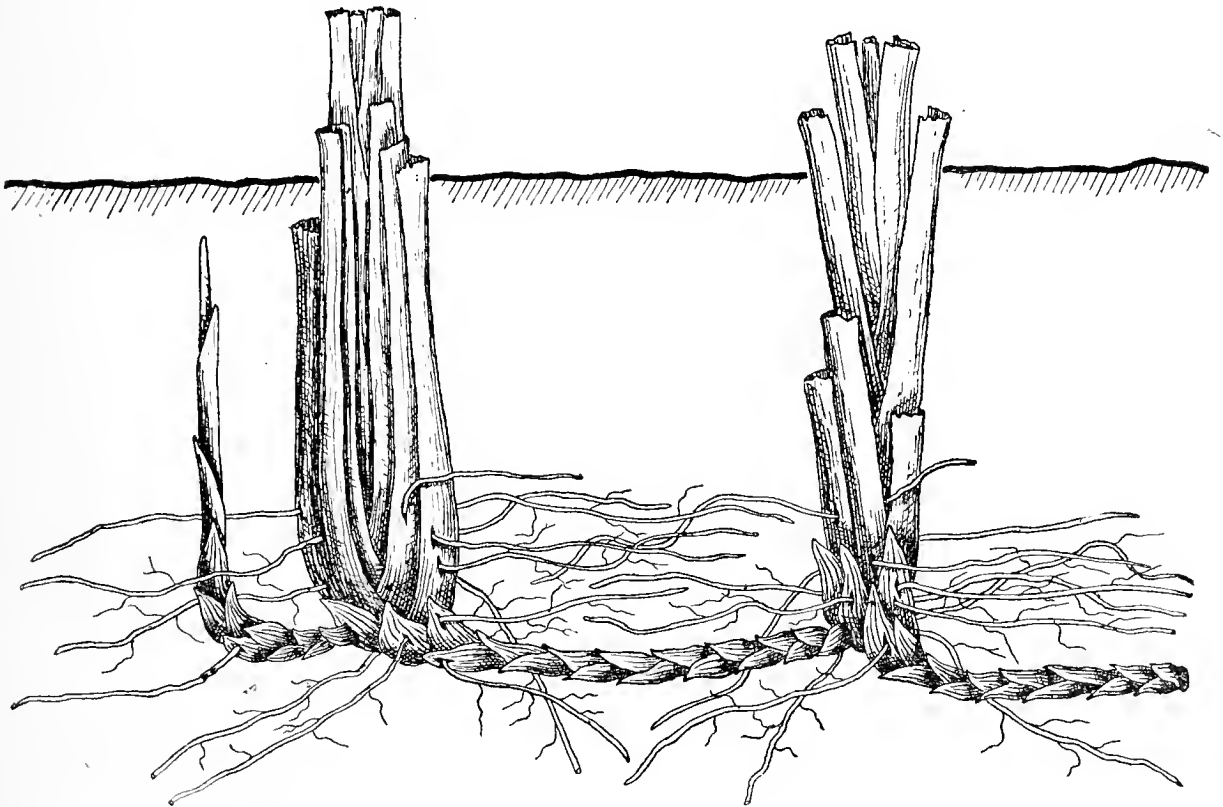
¹ Cf. Hall, *The Soil*. 1904. p. 66.

² Wallis, *l.c.*, p. 221.

Früh & Schröter, *l.c.*, pp. 14 and 15.

frequent amongst marsh plants (Text-figs. 11, 12, 14 and 15). This leads, in the case of a practically closed "formation" such as Wicken Sedge Fen, to an almost inextricable tangle of roots, rhizomes, stolons, &c., just below the surface of the soil.

Although in general the subterranean organs of marsh plants are placed comparatively near the surface, yet the depths at which these parts are buried may vary considerably. It depends in any given case partly on the species of plant, and partly on the water content of the soil. Thus the rhizomes, &c., of the more definitely wet-marsh plants may, if growing actually in shallow water, creep on the surface of the underlying mud. But if growing in the drier parts of the Fen, they are frequently placed at considerable depths in the soil. For instance, in the drier parts the rhizome of *Cladium* is generally found at a depth of six to nine inches (Text-fig. 12), and



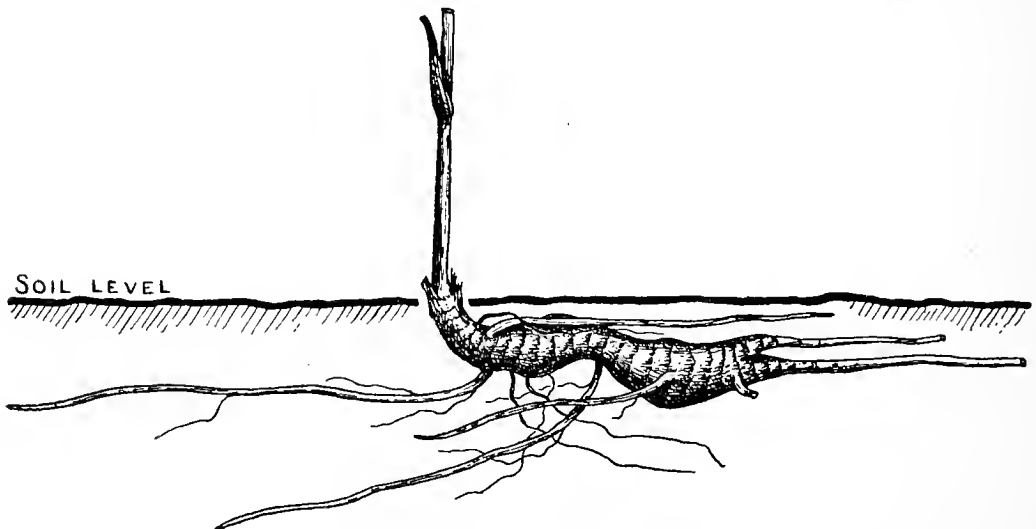
Text-fig. 12. - *Cladium Mariscus*, in moderately damp soil (September).
X $\frac{3}{8}$.

that of *Juncus obtusiflorus* is often buried three to five inches (Text-figs. 11 and 15). A "wet plant" then, growing on a "dry island," can easily adjust itself by placing its rhizome at a lower level. To put it more correctly, the plants have probably become first established in the damper soil, and have subsequently crept into the drier parts by undermining them, and then sending up their

shoots into the air (see Text-fig. 11). The “wet plants” which have creeping stems, and stiff pointed shoots that can easily force their way up through the overlying soil &c., are those best adapted for this invasion of the drier areas. It is generally such plants, e.g. *Phragmites* and *Juncus obtusiflorus*, that one actually finds in these cases. The “dry plants” on the other hand, are much more rarely able to endure the conditions found in the wetter parts of the marsh. A reciprocal invasion does occur, however, and will be described later in this paper.

Thus the wettest parts of the Fen are occupied only by “wet plants”; the drier parts chiefly (though not exclusively) by “dry plants”; while the intermediate places, where the average water level is, say five inches or more below that of the soil, may contain a complicated mixture of wet, intermediate and dry forms. In the latter case the underground parts are adjusted at different levels according to the idiosyncrasies of the plants themselves.

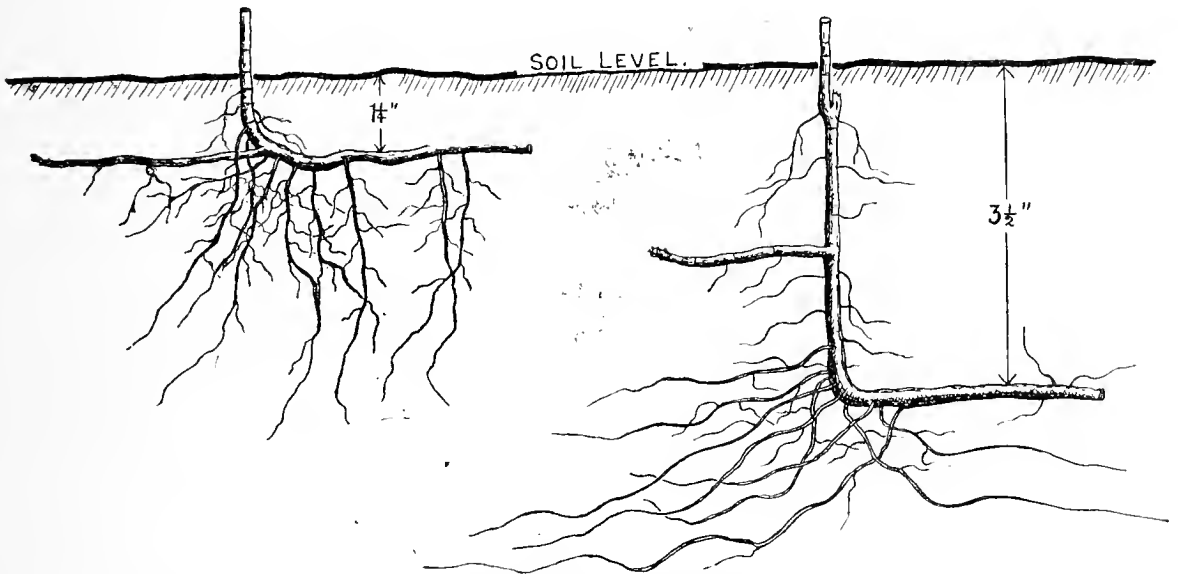
The underground parts hitherto mentioned have been chiefly stems, but the roots also require some mention. Speaking generally, there is a marked tendency for the roots of the Fen plants to be placed more or less horizontally in the soil (Text-figs. 12, 13 and 14). This may apply in the case of Dicotyledones, to the primary as well



Text-fig. 13. Young plant of *Peucedanum palustre*. $\times \frac{2}{3}$. (September).

as the lateral roots (e.g. *Peucedanum palustre*, Text-fig. 13). “Dry plants” living in a relatively damp soil exhibit this tendency to a very high degree, their roots often creeping amongst mosses, &c., actually on, or only partly beneath the surface. But “wet plants” also frequently show a similar method of root growth, e.g. *Cladium* (Text-fig. 12). The direction of growth of the roots would seem to be

largely determined by the water content of the soil; as a given plant often has more or less vertical roots when growing in a fairly dry soil, while in a wetter one its roots grow much more horizontally. Compare the relative positions assumed by the roots of *Lysimachia vulgaris*, when growing at different depths in a moderately damp soil (Text-fig. 14). This phenomenon is doubtless correlated with the paucity in oxygen of the more waterlogged soils.



Text-fig. 14. *Lysimachia vulgaris*. These two plants were found growing near each other in moderately damp soil. $\times \frac{1}{4}$. (September).

As pointed out above, many plants possess a very wide moisture range. *Hydrocotyle vulgaris* for example, may occasionally be found submerged, at other times it will grow on fairly dry exposed peat banks. *Cladium* again may grow (as commonly in the Norfolk Broads) actually in water, though at Wicken it is generally found under intermediate moisture conditions. On one occasion I found a dwarfed specimen of this plant growing quite contentedly on the top of a dry mound of peat, some two feet above the surrounding soil. Again, I have succeeded in growing quite vigorous specimens of *Spiraea Ulmaria*, which is a dry-Fen plant, with their rhizomes submerged in water; while *Lythrum Salicaria*, a relatively "wet plant," will grow luxuriantly in ordinary garden soil.

But although individuals can readily adapt themselves to considerable variations of habitat, yet in nature one seems to rarely meet with these plants in anything like the extreme positions which they are capable of occupying. For instance, although *Spiraea* will grow and even flower, with its rhizome submerged, yet I do not remember finding a single specimen naturally growing in really

waterlogged soil. Miss Stopes also, in describing "The Colonisation of a Dried River Bed,"¹ mentions that *Spiraea Ulmaria*, though growing in great numbers on the bank, did not begin to invade the river bed until the second year after the diverting of the stream. By this time the bed was almost dried up.

Possibly two factors at least are concerned in this limitation so commonly found in nature :—

(1). Competition. The moisture conditions under which a species is usually found, may be those in which it can most successfully resist the attacks of competing species. Some plants however, when once established, are able to resist attack, even if the physical conditions change, much more than others. Thus *Phragmites*, with its deeply placed rhizomes, and spear-like spring shoots, which can force their way up through the overlying plants with comparative ease, will hold its own for a long time, even if the superficial layers of the soil become dry. Plants of a different habit of growth however, such as e.g. *Alisma Plantago*, succumb much more readily.²

(2). It is probably decided in many cases during the early stages; *i.e.* germination of the seed and growth of the seedling. Obviously, if the conditions are such as are very unfavourable to the young plant, there is but a poor chance of its surviving to the adult state.

It would be interesting to put this matter to the test of experiment.

It was mentioned earlier that, although invasion of dry places by "wet plants" was the more obvious, yet a reciprocal invasion by the "dry plants" did occur. We have seen that many of the Fen plants have creeping underground parts; but a tufted or caespitose habit is not uncommon. *Molinia coerulea* is one of the most striking examples of this. A good many Carices have a similar habit, while not infrequently, mixed tufts of *Juncus obtusiflorus* and *Carex* sp. are to be found in the wetter parts (Text-fig. 15). Mosses appear on these tufts, and form a dense growth binding the dead leaves, &c., together. Particles of soil and other debris may be washed in, and gradually the level of the clump is raised. When this is sufficiently high and dry, it forms a convenient germinating place for seeds of other plants, which are thus able to establish themselves above the damper parts of the soil. Seedlings of *Lythrum*, *Spiraea*,

¹ Stopes, New Phytologist, Vol. II., 1903, pp. 188 and 191.

² Stopes, *l.c.*, pp. 188 to 192.

Molinia and other more or less "dry plants" can often be found under such conditions (Text-fig. 15).

Judging from the seedling plants most commonly found on Wicken Fen, it would seem that on the whole, the Monocotyledones reproduce themselves by seed much less frequently than the Dicotyledones. And further, the "dry plants" are apparently



Text-fig. 15. A mixed tuft of *Juncus obtusiflorus* and *Carex* sp., growing on wet soil and showing invasion by "dry plants." The seedlings on the moss (from left to right) are:—*Molinia*, *Lysimachia*, *Spiraea*, *Lythrum*, *Spiraea*. W, water level in September. $\times \frac{1}{6}$.

increasing by this means much more rapidly than the "wet plants." Perhaps the commonest seedlings are those of *Spiraea Ulmaria*, but *Rhamnus Frangula*, *Lysimachia vulgaris*, *Thalictrum flavum*, *Lythrum Salicaria*, &c., are also abundant.

CHANGES IN THE VEGETATION.

It is probable that in Britain generally, the prevailing climatic conditions are less favourable to the rapid growth of peat than formerly.¹ Indeed, so far as the Fenland is concerned, some writers maintain that peat-formation has practically ceased.² Others say that "if peat is only removed down to water level, it at once begins to grow again, and grows at the rate of a foot in twenty years."³ In any case, on Wicken Sedge Fen the peat is certainly not being denuded, as it is in many parts of Scotland, &c.⁴: and though the upward growth may be slow, it can scarcely be doubted that the level is gradually, if slowly, rising, and therefore becoming drier, by the accumulation of plant remains.

Moreover, not only is Wicken Fen surrounded for the most part by comparatively dry lands; but owing to the system of lodes connected with it, inundations are probably much more rare than formerly. Thus Wicken Fen is almost undoubtedly, as the older Fenmen assert is the case, becoming gradually drier.

Again, apart from the sweeping changes in the flora brought about by the draining of the Fens, it is well known that the flora of Wicken Fen itself has undergone changes in quite recent times. In addition to the disappearance of some of the rarer species, certain of the plants mentioned in Babington's list of Wicken Fen plants⁵ would appear to be less common now than formerly.⁶ For example, *Schœnus nigricans* is given in the list as one of the commonest plants. It is still abundant at Chippenham Fen, but at Wicken I have only seen a single tuft, by the side of Wicken Lode.

¹ Lewis, The Sequence of Plant Remains in the British Peat Mosses, Science Progress, Oct. 1907, p. 2.

² Miller & Skertchly, *l.c.*, p. 556, and Reed, *l.c.*, p. 224.

³ Fearnside, The Geology of Cambridgeshire (in The Nat. Hist. of Camb., ed. Marr & Shipley), p. 49.

⁴ Lewis, *l.c.*, p. 3.

⁵ Babington, Flora of Cambridgeshire, 1860, pp. 312 to 313.

⁶ On the other hand, *Epipactis longifolia* and *Myrica Gale*, which Babington (*l.c.*, p. 314) mentions as absent from Wicken Fen, are now to be found there. Of course a number of other additions could be made to Babington's list.

Again, Mr. G. H. Verrall said, in a letter written last year,—“Considering the remarkable change, it may interest you to know that when I first saw the Fen in 1875, it was almost a mass of *Thalictrum flavum*, which is now comparatively uncommon.”

But perhaps the most far reaching change of all is the apparently rapid increase in the number of bushes.¹ As this may herald important changes in the not very distant future, the subject will be treated in some detail.

Dotted over the Fen are numbers of bushes. While comparatively few on the western portion, towards the north-east they are so abundant as to form large and continuous thickets. The following are the woody plants which occur on Wicken Fen:—

Salix cinerea, *S. caprea*, *S. repens*, var. *fusca*, &c.; *Myrica Gale*; *Betula alba*; *Rhamnus Frangula*; *Viburnum Opulus*. All these are well known as moisture-loving species, and are frequent components of marsh-thickets.² *Alnus glutinosa*, though common enough at Chippenham Fen, and also as one of the constituents of the buried forests of the Fenland,³ appears to be entirely absent here.

In addition to the above, the following species, less commonly associated with very damp soils, are to be found:—*Crataegus Oxyacantha*, *Rhamnus catharticus* and *Ligustrum vulgare*.

Several specimens also of *Pyrus Aucuparia* occur; a rather large ash (*Fraxinus excelsior*) is to be seen on St. Edmund's Fen, while on the Sedge Fen, growing directly on the peat, is a solitary young *Quercus*.

The commonest species of all is *Rhamnus Frangula*. Between the centre of the Fen and Wicken Lode village this species alone forms many extensive thickets; so dense that practically all other vegetation is excluded. The great number of seedlings and young plants of various ages which are found not only bordering these thickets, but elsewhere on the Fen, bears witness to the rapid rate at which this species is increasing. Its fleshy fruits are readily eaten by birds, and seeds frequently found in bird-droppings afford evidence that this is a common means of dispersal.

Salix fusca also forms extensive growths in some parts. But apart from the two cases just mentioned, elsewhere on the Fen it is very usual to find the bushes growing in mixed clumps. Such a

¹ Cf. Wallis, *l.c.*, p. 220.

² Warming, *l.c.*, p. 173; and Fröh & Schröter, *l.c.*, pp. 414 *et seq.*

³ Miller & Skertchly, *l.c.*, p. 567.

group of bushes may include a *Rhamnus* or two, a *Viburnum*, and perhaps a couple of species of *Salix*. This grouping of the bushes may perhaps be largely influenced by the periodic cutting of the sedge. The young bushes are cut with the sedge so long as they offer no great resistance to the cutters. Many are perhaps killed in this way, while others form coppiced growths. When however, a bush is large enough to interfere with the cutting, it is left alone, and so may attain maturity. Immunity from cutting will be more frequent when several bushes are growing together, and this may account for the mixed character of the clumps. Of course it may be that in other cases a single bush has attained maturity, and beneath its shelter, seedlings of other bushes have been able to grow protected from the Fenman's scythe.

We have seen that Wicken Fen is not in a "primæval" condition. It can scarcely be said to be even in a natural condition. As almost everywhere in our country, man has left even here, his impress on the vegetation. The draining of the surrounding lands, and the embanking of the lodes, have increased the dryness of even Wicken Fen, and introduced many new land plants ready to seize on any available dry spot. The cutting of the sedge, by penalising plants of slow growth and encouraging those of rapid growth, has played its part in more completely mixing up the Fen plants. It has also affected the distribution of the bushes, while the periodic removal of so much of the surface vegetation doubtless slows down the rate of peat formation. But after all, in spite of these artificial modifying influences, events would seem in the main to be following pretty much a natural sequence. A few species may have been introduced and a few exterminated. The vegetation may be more mixed than it would have been if left alone. But still Wicken Fen is now, what it has been before, and what it would sooner or later have become again, a drying-up marsh. And on the whole the process is a natural one.

And now what of the future? There can be little doubt that Wicken Fen is becoming drier, and that the number of "dry plants" is increasing. The bushes are also certainly becoming more numerous, apparently with considerable rapidity. Already a few trees from drier lands, such as mountain ashes and oaks, are invading the Fen. It therefore seems probable that Wicken is on the verge of another forest period, and that sooner or later it will become practically a huge marsh thicket. Then finally, if the Fen is not in the meantime appropriated by man for other purposes, the

Rhamni and Salices of the thickets may once again be replaced by stately forest trees, growing above the spot where their predecessors still lie buried in the peat.

Thus it would seem that Wicken, the last considerable area of Fen vegetation, is once more doomed to dryness. The marsh plants which now grow there will gradually disappear, for they are fighting a losing battle. But, as in the rest of the Fenland, the aquatics will linger on in the lodes, and a few of the marsh species will continue to fringe their banks, long after Wicken Fen itself is dry land. But events move slowly, if measured by years, and all this will take a long time to accomplish. In the meantime, the present vegetation of Wicken Fen presents to the botanist a host of absorbing problems.

DESCRIPTION OF PLATE IV.

ILLUSTRATING PROFESSOR YAPP'S PAPER ON WICKEN FEN.

Fig. 1. Wicken Sedge Fen and Wicken Lode, in July. Landwards the fringing reed-swamp (in front of which is *Castalia alba*, Gr.) passes into the marsh. The latter is seen to be dotted with bushes.

Fig. 2. *Butomus umbellatus* Linn., from a lode near Upware. July.

Fig. 3. Adventurers' Fen in January, showing the long parallel peat trenches, and staeks of eut peat. Trunks and stools of forest trees are frequently unearthed here, during the process of peat-cutting. The trees in the distance are on the drained area south of the Wicken group of Fens.

NUCLEAR FUSIONS AND REDUCTION PHENOMENA
IN THE MYXOMYCETES.

IN the course of a cytological investigation of *Ceratiomyxa*, the sole representative of the exosporous Myxomycetes, Olive has obtained evidence that a fusion of nuclei in pairs occurs prior to spore-formation and that this fusion is followed by a synaptic stage and two nuclear divisions. The course of events described by Olive is as follows:—Fusion of nuclei in pairs occurs towards the close of the cleavage of the protoplasm which precedes spore-formation. The peripheral protoplasm is thus cut up into numerous uninucleate masses which may be called "protospores." Creeping movements now take place in these "protospores" so that each forms a swollen globular end borne on a long stalk. All the protoplasm passes into the globular extremities, the stalks and other supporting structures then consisting of nothing but slime. Olive states that the nuclear fusion referred to above is followed almost immediately by synapsis. His figures show clearly that a contraction of the chromatin thread takes place at this stage. Two nuclear divisions follow directly in rapid succession, but these being unaccompanied by cell-division, each spore at maturity contains four nuclei. Olive looks upon these two mitoses as comparable to the double nuclear division which occurs in spore-mother cells and with which reduction in the number of chromosomes is associated. If this interpretation is correct the single "spore" of *Ceratiomyxa* represents a tetrad of spores of the higher plants.

Jahn² states, however, that a nuclear fusion in *Ceratiomyxa* takes place at an earlier stage than that mentioned by Olive. The former describes a nuclear fusion in the young fruit bodies, this fusion being followed by a contraction of the chromatin which he interprets as synapsis. Shortly before spore-formation two nuclear divisions succeed one another in rapid succession and these Jahn considers to be the heterotype and homotype mitoses. Of the nuclei thus produced, Jahn states that at least half disorganise, while the others form the nuclei of the young spores. During the maturation of the latter two nuclear divisions succeed one another rapidly so that each ripe spore contains four nuclei as described by Olive.

There is thus a marked divergence in the results of these two investigators. Unfortunately Jahn gives no figures, so it is impossible to compare adequately his results with those of Olive. The latter expressly states that he could find no nuclear divisions in the fructifying plasmodium prior to cleavage, and concludes that *Ceratiomyxa* is peculiar in this respect since in other Myxomycetes

¹ Olive, E. W. Cytological Studies on *Ceratiomyxa*. Trans. Wisconsin Academy of Sciences, etc. December, 1907.

² Jahn, E. Myxomycetenstudien—Kernverschmelzungen und Reduktionsteilungen. Ber. d. Deut. Bot. Ges., Feb., 1907.

examined nuclear division occurs either before cleavage, as in *Trichia* or while cleavage is progressing, as in *Fuligo*.

Jahn states also that Miss Helene Kränzlin has observed that a fusion of nuclei in pairs occurs in the young sporangia of *Trichia* and *Arcyria*. Jahn himself finds a similar fusion in endosporous Myxomycetes, followed by a synaptic stage. This is succeeded by a mitosis and then spore-formation intervenes, each spore containing a single nucleus which has entered upon the resting condition. A nuclear division occurs in each spore upon germination and Jahn looks upon this as the second division of the meiotic phase begun immediately before spore-formation.

If this interpretation of the nuclear phenomena in the endosporous Myxomycetes is true we have the extraordinary occurrence of a prolonged resting period between the heterotype and homotype divisions.

Reduction divisions are now known to occur in many Algæ and Fungi as well as in some Protozoa, so that the meiotic phase seems to be of widespread occurrence in the lower as well as in the higher organisms.

F. T. B.

A CONTRIBUTION TO A NEGLECTED BRANCH OF BOTANY.

VISITORS to the Palæobotanical Museum in the Jardin des Plantes, Paris, or to the Geological Museum in the Sorbonne may have noticed the specimens of flowers with perianth, stamens, and carpels from the Lower Eocene freshwater deposits of Sézanne. These relics of a Tertiary Flora, which are among the most striking examples of incrustations, have as yet been only partially investigated. The late Professor of Geology at the Sorbonne, Prof. Munier-Chalmas, a man of exceptional ability, devoted a considerable time to the Sézanne material, but like other men of genius he could rarely be induced to communicate his results to the scientific world. The travertine of Sézanne, formed by the deposition of calcareous material on the banks of a Tertiary river which flowed between Chalk cliffs, contains numerous fragments of plants which may be reconstructed as casts by introducing wax or plaster into the cavities originally occupied by the flowers and other fragments and removing the surrounding matrix by hydrochloric acid. The late Marquis of Saporta¹ and, more recently, M. Langeron² have made us familiar with many of these travertine plants, but the more complete specimens prepared by Munier-Chalmas are still undescribed; it is, therefore with considerable satisfaction that we welcome the publication of a paper by M. Viguié in the current number of the "Revue Générale

¹ Saporta, Mém. soc. géol. France [2] VIII. mém. 3., 1868.

² Langeron, Bull. soc. d'hist. nat. d'Autun, 1899, 1900.

³ Viguié, Rev. gén. Bot. XX., 1908, p. 6.

de Botanique" entitled "Recherches sur le genre *Sezannella*." The generic name *Sezanella* was proposed by Munier-Chalmas for specimens of flowers and fruits; the flowers, referred to two species, *Sezanella major* and *S. minor*, are characterised by the possession of a polyphyllous perianth composed of five large oval sepals, valvate in bud, alternating with five stamens with unusually long anthers dehiscing porocidally. The ovary is formed of five concrescent carpels with axile placentation containing two rows of horizontal ovules; the slender style, three to four times the length of the ovary, terminates in a capitate stigma. The fruit is a spherical capsule with septicidal dehiscence 1-2 cm. in diameter. Another feature worthy of notice is the prolongation of the pedicel of the flower as a column on which the ovary and androecium are borne. Some of the floral characters suggest comparison with the Malvaceæ, but it is to the Lasiopetaleæ, a tribe of the Sterculiaceæ, and to the two genera *Lysiopetalum* and *Lasiopetalum* that M. Viguier considers the fossil species to be most closely allied. Certain leaf-impressions described by Saporta as *Pterospermites inæquifolius* may possibly represent the foliage of *Sezanella*. With the exception of the two West Australian genera with which *Sezanella* is compared the Sterculiaceæ are tropical in their distribution. If, therefore, the conclusions of M. Viguier are correct, they form a particularly interesting contribution to our knowledge of plant-geography recalling Unger's statements, based on evidence which was justly called in question by Bentham,¹ in regard to the presence of Australian types in Tertiary Europe.

There can be little doubt that a thorough study of Tertiary plants would throw considerable light on the past history of Angiosperms. It is unfortunate that the nature of the records of Flowering plants has led to an unnecessarily pessimistic attitude on the part of many botanists towards investigations in this department of Botany; we know that the enthusiasm of some of the earlier writers has been responsible for the publication of lists of species founded on wholly inadequate data, but this is hardly a sufficient reason for the neglect which Cretaceous and Tertiary fossils have suffered in recent years at the hands of European botanists. No sane person is likely to dispute the inferiority of casts and impressions to petrifications; but to condemn as useless the less promising material suggests partial acquaintance with the facts or lack of enterprise.

A. C. SEWARD.

¹ Bentham, Presid. Address, Linn. Soc., 1870, pp. 12 *et seq.*

THE

NEW PHYTOLOGIST.

VOL. VII., Nos. 4 & 5.

MAY 31ST, 1908.

A CONTRIBUTION TO THE ANATOMY OF *GINKGO*
BILOBA.

BY F. J. F. SHAW, A.R.C.S.

(WITH TEXT-FIGS. 16—18).

NOTWITHSTANDING the numerous speculations upon the morphological nature of the "collar" in the ovule of *Ginkgo* none appears to have been based upon an adequate anatomical investigation of the organ in question. Most have been derived from a study of malformations, the phylogenetic value of which many modern botanists are disposed to doubt. It is hoped that the results put forward in the present short note may furnish a new standpoint from which to view the problem.

The material consisted of about a dozen specimens of the female "flower" preserved in spirit. All the specimens showed two ovules, one fertile and one small aborted sterile ovule. The sections were cut by hand, stained with safranin, and mounted in glycerine jelly. Subsequently a model of the xylem was built up from the sections, after the method employed by Farmer and Hill in the case of *Angiopteris*.

VASCULAR SYSTEM OF FEMALE FLOWER.

As is well known, the female "flower" consists of a stalk or peduncle bearing two lateral stalked ovules. A series of transverse sections was cut from the base of the peduncle up into the fertile ovule.

A transverse section taken from as near the base of the peduncle as the specimens allowed shows a ring of four collateral bundles, the bundles being definitely associated in pairs. A little higher up in the peduncle, the two bundles of each pair unite and form two collateral bundles facing one another (Text-fig. 16, 1).

Of these two bundles one is concerned with the vascular supply of the fertile ovule and the other with that of the frequently sterile

Text-fig. 16. Phloem is cross-hatched, tracheids cut transversely represented by series of dots, cut longitudinally by lines. Position of sterile ovule shown thus—X.

A=bundle of fertile ovule ; B=bundle of sterile ovule ; V=anomalous tissue ; C=cambium ; H="horns" ; T.L.=tracheids cut longitudinally ; T.S.=tracheids cut transversely ; M=metaxylem ; K=crushed parenchyma between two phloems ; D=place where "horns" unite. PX=median plane of the pair of ovules.

Transverse sections.

1. Bundles in peduncle.
2. Single bundle in pedicel—points of origin of anomalous tissue marked by two dots.
- 3, 4. Lower part of collar—anomalous vascular tissue present.
5. Commencement of approximation of "horns"—some tracheids cut longitudinally.
- 6, 7, 8. Union of "horns"—inverted vascular bundles splay outwards in the top of the collar.
9. Single concentric bundle in base of ovule.
- 10, 11. Splitting of bundle giving rise to two concentric bundles.

ovule. The latter is usually small and in its passage up the peduncle gradually dwindles away and becomes lost in the mass of parenchyma and "transfusion tracheids" forming the bulk of the ground-tissue. In some cases in which the sterile ovule has developed to a rather greater extent this bundle can be traced as running definitely into it. It may be remarked that, as we proceed up towards the ovule, we find a gradually increasing number of "transfusion tracheids" intermingled with the ordinary parenchyma. These "transfusion tracheids" are short and are reticulately thickened; they form a very characteristic feature of the sections.

One of the bundles has now been disposed of and we pass to the consideration of the other, which will eventually give rise to the vascular system of the large fertile ovule. In a section taken at the base of the collar, just above the sterile ovule, this bundle exhibits normal collateral structure, the xylem facing towards the sterile ovule (Text-fig. 16, 2). On the outer edge of the phloem there is a fairly continuous layer of large, thick-walled, parenchymatous elements stained with safranin. At one or two spots the ordinary parenchyma of the ground-tissue next to these large cells has an abnormal appearance. The cells are smaller, possess dense contents with well-marked nuclei, and appear to be rapidly dividing. The divisions at first take place irregularly in all directions, but a little higher up they begin to assume a definite tangential direction. The result is that at one or two places on the outer side of the main bundle, next the phloem, a dividing cambium is produced. This cambium gives rise to tracheids externally and to phloem internally, and several little vascular bundles with inverted

orientation are seen to be scattered along the outer edge of the main bundle.

Text-fig. 16, 3, represents a section taken from the lower part of the collar. Here there are three anomalous bundles in addition to the main bundle. Moreover in one case the cambium of the main bundle has become continuous round its flank with that of the nearest inverted bundle.

A little higher up, about the middle of the collar, the parenchyma on the other flank of the main bundle also becomes merismatic, and here likewise the cambium becomes continuous with that of the nearest inverted bundle. Text-fig. 16, 4 shows the vascular tissue slightly crescent-shaped, the xylem of the main bundle being on the concave side of the crescent and the xylem of the inverted tissue on the convex. The cambium of the main bundle is continuous with that of the inverted tissue round the "horns" of the crescent—these "horns" face towards the sterile ovule. At the back of the main bundle the inverted tissue consists of two small bundles.

The crescent-shaped condition of the vascular tissue becomes more marked further up towards the ovule. The two "horns" curve round and become much more prominent. So rapidly does this take place that the tracheids of the main bundle and of the inverted xylem at the "horns" run nearly horizontally through the parenchyma and are hence cut longitudinally in the transverse sections. The cambium remains continuous round the "horns" during this process (Text-fig. 16, 5 and 6). In Text-fig. 16, 7, the cambium of the inverted tissue appears continuous right round the convex side of the crescent. The space between the two cambiums is filled with phloem, and it is difficult to draw a line of demarcation between the phloem of the inverted tissue and the normal phloem, but remnants of large parenchymatous cells can sometimes be discerned between the two. The tracheids of the inverted tissue are, on the whole, running outwards towards the periphery and are cut longitudinally right round the outer edge of the crescent. The parenchyma enclosed between the "horns" is intermingled with numerous tracheids and forms a sort of metaxylem. As regards the main bundle the tracheids of this metaxylem are centripetal.

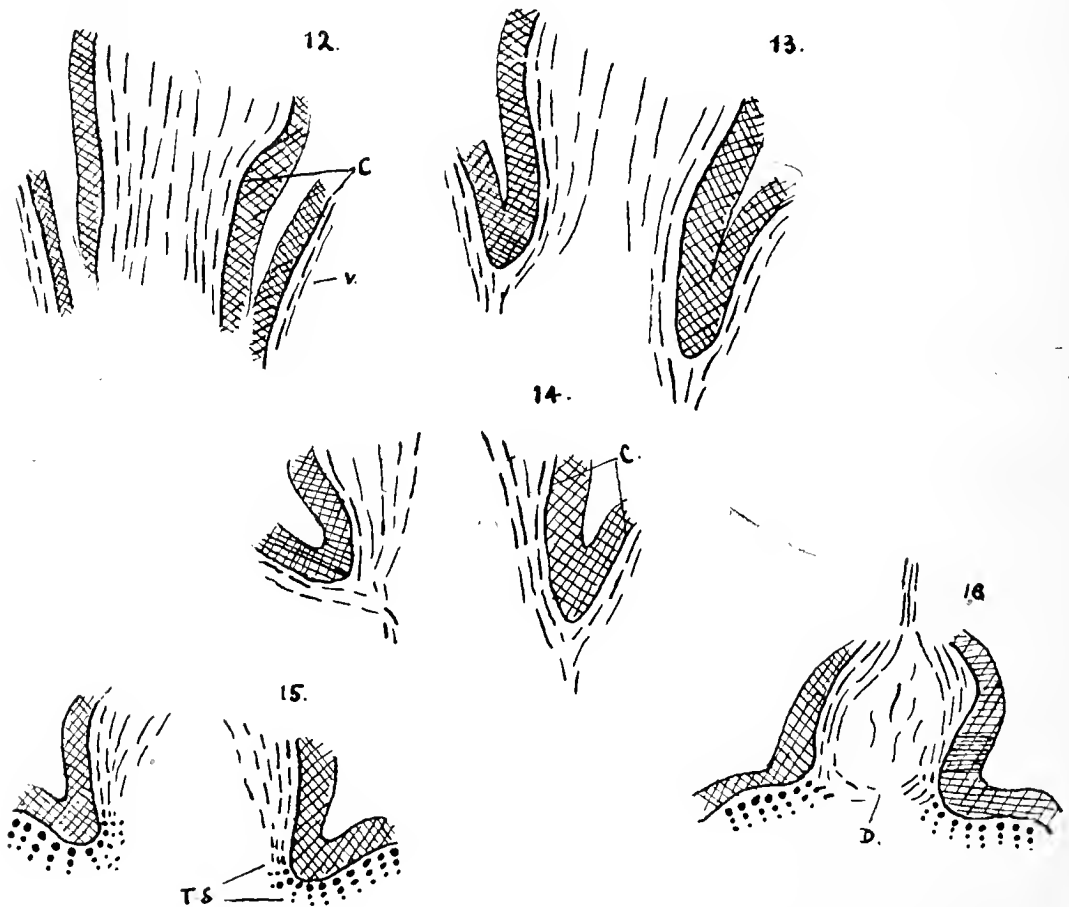
In the upper region of the collar, the inverted tissue continues to splay outwards and disappears from the transverse sections; it persists longest at the "horns" (Text-fig. 16, 8). The tracheids of the main bundle at each "horn," those on the inner side of the crescent, continue to run almost horizontally, and higher up in the collar they

gradually approach one another. At the extreme top of the collar they meet and the cambium of the main bundle becomes continuous all the way round (Text-fig. 16, 9). The number of "transfusion tracheids" in the general parenchyma is very large at this level. A single concentric bundle is thus formed at the base of the ovule; its central part consists of the metaxylem, mentioned above, and it is enclosed by the genuine xylem of the bundle. The latter shows a marked tendency to aggregate at two points on opposite sides of the bundle (Text-fig. 16, 9). The tracheids in one half of the bundle all appear to be running towards the region where the "horns" have recently united, in the other half of the bundle they trend towards a point exactly opposite. This behaviour of the tracheids is a foreshadowing of the splitting of the concentric bundle which takes place a few sections higher up in the ovule. Seeing that the two "horns," which united to form the concentric bundle, faced towards the sterile ovule, it is plain that the separation of this bundle into two takes place at right angles to the plane of the ovules—the two resulting bundles lying in that plane (Text-fig. 16, 10). They rapidly divaricate and become first horseshoe-shaped and then mesarch and concentric (Text-fig. 16, 11). Ultimately they die out after passing up the side of the megaspore cavity for some little distance.

The essential feature to which attention is drawn consists in the development of anomalous vascular tissue, with inverted orientation, throughout the region of the collar. This tissue is strictly confined to the collar and takes no part in the vascular supply of the ovule.

Besides the anomalous tissue the peculiar manner in which the main bundle becomes concentric is worthy of notice. Stress has already been laid on the fact that throughout this process its cambium remains continuous with that of the anomalous tissue; *i.e.*, while the "horns" approach one another, during the passage of the bundle upwards, the cambium remains continuous round the "horns." Since these approach one another fairly rapidly, as is shewn by the fact that their tracheids run longitudinally in the transverse sections, it follows that a sort of oblique gutter of cambium is formed on either flank of the main bundle. The outer wall of the gutter is the cambium of the anomalous tissue, the inner wall that of the main bundle. A consideration of the description together with the photograph of the model will make this clear (Text-fig. 18).

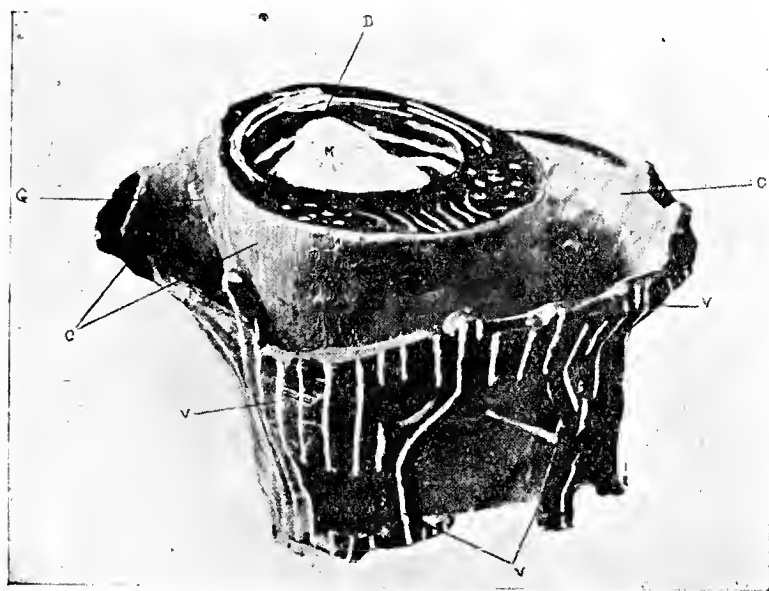
A series of longitudinal sections cut at right angles to the plane of the ovules affords a complete confirmation of the interpretation advanced above. Such a series is of course tangential to the main bundle. The sections begin on the side farthest from the sterile ovule—hence we gradually cut through the main bundle and into the “horns.” In Text-fig. 17, 12 the main bundle is shewn, flanked by two others with inverted orientation. Further across the main bundle the plane of section traverses the region where it is passing into the concentric state. A section here shows the main bundle with two lateral anomalous bundles; the cambium, however, is continuous, the latter appearing as wings of the former (Text-fig. 17, 13); all the tracheids run longitudinally. Here is seen the first indication of the gutter of cambium, filled, of course, with phloem, as described above. In the succeeding sections, approaching the sterile ovule, the distance from the top of the main bundle to the bottom of the gutters decreases, this shows that the gutters are running obliquely upwards through the collar (Text-fig. 17, 14 and 15).



Text-fig. 17. Longitudinal sections (tangential).

- 12, 13, 14. Sections passing through main bundle towards sterile ovule—cambium of main bundle continuous with that of anomalous tissue.
15. Tracheids of anomalous tissue and those of main bundle at the “horns” cut transversely.
16. Union of “horns”—above, the main bundle is giving rise to one of the smaller concentric bundles in the ovule.

It will be remembered that in describing the transverse sections it was pointed out that the tracheids of the "horns" were cut longitudinally. In the longitudinal sections these are of course cut transversely (Text-fig. 17, 15). It is easy to realise how, during the transition of the main bundle to the concentric state, the anomalous tissue encircles the newly-formed half of the main bundle. The



Text-fig. 18. Photograph of model of vascular tissue in collar, model shows xylem only and is viewed from above and behind. "Horns" of main bundle point away from, and anomalous tissue points towards observer; white lines show curve of tracheids. Area marked M. filled with metaxylem (which is not shown in the model), hence the union of "horns" can be seen at D; the lighter area C is the cambium. Note on one side the oblique gutter G caused by union of cambium of the anomalous tissue with that of the main bundle.

tracheids of the main bundle belonging to the "horns" are also cut transversely, and they are situated at the base and inner side of the gutters. The union of these tracheids, when the main bundle becomes concentric, is shown in Text-fig. 17, 16. Here they are seen running from either side of the main bundle across it to the centre, and at right angles to its length.

CONCLUSIONS.

The occasional occurrence of an apical bud between the ovules, and the general anatomy, force us to consider the peduncle as a shoot bearing two lateral stalked ovules. Each ovule is attached to the peduncle by a short pedicel, and at the point of union of pedicel and ovule we have the collar. It is however difficult to account for the inverted vascular tissue of the collar if we consider it as a reduced carpel, a view which has often been expressed. The pedicel seems to have a petiolar structure relative to the main shoot, for the single vascular bundle which traverses it has xylem

directed towards what would be the upper surface. The relationship is however obscured owing to the excessive development of one ovule, which comes to lie almost apically. The pedicel passes very rapidly into the collar with its inverted bundles.

Now in the seed *Lagenostoma Lomaxi* it is stated that the pedicel has the structure of a petiole, and, what from our point of view is more important, in the cupule the vascular bundles are often inverted (Oliver and Scott Phil. Trans., Vol. 197 B, 1904). It is only fair to state however that the general impression in the minds of the authors seems to have been that the bundles were, as a rule, normally orientated although there was a considerable amount of variation. At all events for the present we would tentatively suggest that, in the light of anatomical investigation, the collar of the ovule in *Ginkgo* is better regarded as a vestigial cupule than as anything in the nature of a carpel. Perhaps when our knowledge of the Pteridosperm seeds with cupules is more extended we may find some in which the cupular bundles were, as a rule, inversely orientated.

In this connection it is interesting to note that at the base of the seeds of certain Cycads (*C. revoluta*, *C. Rumphii*) we have a state of affairs closely paralleled in the collar of *Ginkgo*, the single vascular bundle supplying the ovule being accompanied on its outer convex side by a number of inversely orientated strands (Worsdell, Annals of Bot. XII., 1898, Pl. XVII., Fig. 4). It seems therefore as if both *Ginkgo* and the Cycads might have been derived from forms with cupuliferous seeds, a conclusion which coincides with other evidence. By some writers the collar has been considered as an outer integument, but if we are to look for an outer integument in the lower Gymnosperms we are much more likely to find it in the double nature of the real integument of *Ginkgo* and the Cycads than in the "collar" of the former, which appears to be essentially a "cupule," an organ *sui generis*.

Of course it may be urged that the vascular bundles described in the present paper simply indicate that *Ginkgo* originally possessed a vascular structure similar to that of the Medulloseæ. This view however would take no account of the peculiar situation of the anomalous tissue and, further, it offers no explanation of the "collar." It should also be remembered that the seed is a large one, and this fact, taken in conjunction with the large development of "transfusion tracheids," renders it possible that the presence of additional vascular tissue may have a physiological, rather than a morphological, significance.

THE PHYLOGENY AND INTER-RELATIONSHIPS OF
THE PTERIDOPHYTA.

A CRITICAL RÉSUMÉ.

BY LADY ISABEL BROWNE.

INTRODUCTORY.

THE object of the present series of articles is to place before the botanical student a critical, though brief, account of the principal views now held as to the phylogeny and affinities of the Vascular Cryptogams. During the last few years there has accumulated a great wealth of facts and theories concerning the fossil and recent Pteridophytes and their connection with one another, but no comprehensive review dealing critically with these facts and theories has yet appeared. It is therefore proposed to consider successively the inter-relationship of the various types composing each phylum or main division of the Vascular Cryptogams, and the affinities of the phyla to one another.

I.—SPHENOPHYLLALES.

It will be convenient to begin this *résumé* by a comparison from the phylogenetic point of view of the different members of fossil Sphenophyllales. These forms had an exarch cauline stele, which was triarch, hexarch or dodecarch; the leaves were nearly always some multiple of three; such numbers as eight, recorded by Mr. Seward (10) in *Sphenophyllum emarginatum* being exceptional and possibly due to imperfect preservation. Simple, and repeatedly dichotomous, leaves occur, sometimes on the same stem. Professor Lignier (7) has suggested that the simple leaves are the ultimate segments of a smaller number of dichotomous ones, and that the primitive number of these compound leaves was three. The following quotation will best explain his view of the Sphenophyllaceous leaf: "This leaf always shows at least two separate lobes, which are usually erroneously considered each to represent a leaf But it also happens that the lobing may be greater, and being moreover very deep, separates from one another over the surface of the stem a larger number of segments, each of which simulates an independent leaf; these segments may, according to the case in

question, be, as is usually the case, dichotomously divided, or sometimes quite simple. It is all these variations that have caused the whorls to be described as consisting of six or of another multiple of three.

But whatever the apparent complexity of the whorl the real presence of these leaves can always be demonstrated, thanks to the structure of the node in which there are never more than three meriphytes" (7).

This theory is the most satisfactory that has yet been put forward in explanation of the differences between the leaves of closely related species and even of identical specimens. Dr. Scott has acceded to it (9). Professor Lignier's theory naturally leads us to consider the triarch steles more primitive than the hexarch ones or the dodecarch one of *Cheirostrobis*. The peculiar heterophylly of certain species of *Sphenophyllum* tends to confirm Professor Lignier's theory, for in them the six leaves are in pairs, and one pair is different from the two others (10). This peculiar kind of heterophylly is clearly secondary.

The fructifications of the Sphenophyllales are cones consisting of superposed whorls of sporophylls. There are five principal types of sporophyll; firstly there is the ill-understood type of *Sphenophyllum majus* and *S. trichomatosum*, in which one or more sporangia appear to be situated on the upper surface of the divided sporophyll; then there is the well-known type of *S. Dawsoni* in which two sporangiophores, or pedicels provided with vascular tissue, each bearing a single pendulous sporangium, are inserted on the upper surface of each sporophyll. In another type, that of *Sphenophyllum (Bowmanites) Römeri*, each of the more massive sporangiophores terminates in a peltate projection bearing two sporangia. In *S. fertile* the sporangiophores also bear two sporangia, but the sporophyll is divided into several sporangiophores, some being dorsal and others ventral; there are thus no sterile segments. Finally in *Cheirostrobis* the three dorsal segments of each sporophyll are sterile, while three ventral ones are peltate sporangiophores, each bearing four sporangia.

There are great difficulties in the interpretation of these fructifications. Professor Bower regards the sporangiophore as an organ *sui generis* and not as a leaf or part of a leaf (3), (4). M. Lignier and Dr. Scott regard it as a lobe of the sporophyll or bract (7), (9); while Miss Sykes has recently asserted its cauline nature (11). Professor Bower points out that the chief reasons given

for regarding the sporangiophores as the homologues of the leaves or bracts are the similarity of these organs at their first origin, the similarity of their position on the axis, and the occurrence, in the allied Equisetaceæ, of forms of appendage intermediate between the leaf-teeth and the sporangiophores. Professor Bower clearly shows by his examples of the similarity at origin of such different parts as the sorus and leaf-margin of *Angiopteris* that though such similarity of origin generally obtains in homologous parts, it is not of itself proof of homology; his further examples that prickles and leaves, parts of different morphological nature, have a similar position relative to the axis, also shows that though similarity of position is frequent in homologous organs it cannot be held to prove homology. Professor Bower is probably correct in regarding the Equisetaceous annulus as a reduced leaf-sheath and in no way intermediate between the leaves and sporangiophores, for its teeth show no resemblance to the sporangiophores. So far Professor Bower's arguments in support of the *sui generis* nature of the sporangiophore are founded on negative evidence, but he proceeds to attack the homology of the bracts and the sporangiophores on the ground that the numerical proportion and the relative position that the latter bear to the former are not constant, especially in the allied phylum of the Equisetales. As it seems to be generally admitted that the Equisetales and Sphenophyllales are closely allied and that their sporangiophores are homologous (6), (7), (9), (4), this is a legitimate objection. The numerical proportion of bracts and sporangiophores being inconstant does not seem a serious objection to the view that the latter represent leaf-lobes, for by analogy with the leaves we may well suppose that some and not all of the lobes of the bracts increased by the separation of ultimate lobes of a compound bract. Moreover Professor Bower himself supports the view of a fission of sporangiophores in the Sphenophyllales (3), (4). But he grounds one of his objections on an analogy with *Calamostachys*, a fossil cone belonging to the Equisetales, and consisting of equi-distant whorls of sporangiophores and bracts. Professor Bower points out that if the sporangiophores were leaves it might be expected that "the alternate succession of the sterile leaves would be disturbed where the sporangia intervene between them" (4), whereas each category of appendage, sporangiophore and bract, is inserted with reference to the whorls of its own category of organ and independent of the other whorls. This arrangement of the parts of the cone

in *Calamostachys* is certainly a very strong argument in support of the non-phyllome view of the sporangiophore; but it has been shown that shifting of the position of the sporangiophores has certainly taken place in *Palæostachya* (5), another member of the Equisetales, and this shifting *may* also explain the arrangement of the parts in *Calamostachys*. The course of the vascular bundles supports this suggestion, for the vascular supply of the sporangiophore is, even in *Calamostachys*, where the sporangiophores stand mid-way between the whorls of bracts, given off from the cauline stele at the same point at which the bract-traces originate. But the principal reason for rejecting Professor Bower's theory is that it does not give any adequate explanation of the structure of *Sphenophyllum fertile*, in which the dorsal lobes (Professor Bower's bracts) resemble the sporangiophores and bear sporangia of a perfectly normal type. Dr. Scott regards the fertility of the dorsal lobes as a secondary modification. This is perfectly legitimate for Dr. Scott, since he asserts the homologous origin of the sporophyte, but when it is acceded to by Professor Bower, one of the most convinced supporters of antithetic alternation, it appears to be much strained. It is surely illogical of Professor Bower, who has maintained at great length that the leafy sporophyte arose by progressive sterilization and elaboration of the zygote (1) (3), to suppose that pre-existing vegetative parts, such as bracts, suddenly became sporangiferous. He might of course regard this as a case of atavism, since the whole sporophyte is, according to him, sterilized spore-producing tissue; this would indeed be a strained interpretation, for the bracts represent tissue that has, on his view, been sterilized for an immense period; in fact he regards these appendages as having been sterile ever since they arose. But even this possible, though fantastical, explanation does not account for the fact that this sporangium-bearing bract of his assumes all the characters of a sporangiophore. On the whole then it seems a fair conclusion that parts, such as the dorsal and ventral sporangiophores of *Sphenophyllum fertile*, having a similar position relative to the axis, being apparently identical in structure and function, and bearing certain well-defined identical organs (sporangia) are homologous. There are of course difficulties in applying Dr. Jeffrey's and Dr. Scott's theory (that the sporangiophores of typical Sphenophyllales are the ventral lobes of the sporophyll) to some members of the phylum; such types as *Sphenophyllum majus* and *S. trichomatosum* appear to have no sporangiophores. These may, on this theory, be accounted

for in three different ways. First, small and reduced sporangiophores may have been present and may be unrecognizable in the specimens known to us, which are merely impressions. Secondly the reduction, foreshadowed in the last sentence, may have been carried so far that no traces of the sporangiophore remain. Thirdly it is possible that the so-called sporophyll of these types is in reality a lobe or sporangiophore of a sporophyll, and that these lobes, both of which must have been fertile as in *S. fertile*, have been separated from one another and now belong to successive whorls. This theory may appear strained, but in view of the fact that shifting of the sporangiophore has undoubtedly occurred in the allied phylum of the Equisetales it affords a perfectly legitimate explanation. Miss Sykes has brought forward a theory somewhat similar to Professor Bower's. She differs from him in regarding the sporangiophore not as an organ *sui generis*, but as a cauline structure or branch of the stem; she agrees with him in regarding an axile position of the sporangiophore as primitive, and considers that it has, in the course of evolution, in many cases, been shifted until it became associated with a leaf or bract (11). This theory breaks down over the same difficulty as Professor Bower's, for it affords no explanation of the case of *Sphenophyllum fertile*. If the sporangiophores are cauline, both "ventral" and "dorsal lobes" of Dr. Scott are, in *Sphenophyllum fertile*, cauline, for they are fairly typical sporangiophores, and so far as we know, identical. But these dorsal sporangiophores of *Sphenophyllum fertile* are clearly the homologues of the dorsal "bracts" of the typical species of *Sphenophyllum* and *Cheirostrobos*. These bracts are clearly phyllomes and not cauline structures; Miss Sykes herself admits this for *Sphenophyllum Dawsoni*, but their leaf-like character is even more marked in *Cheirostrobos*. The principal point in favour of Miss Sykes' theory, though one not mentioned by her, is the fact that in *Archæocalamites*, the oldest of the Equisetales, the sporangiophores are borne on the axis; this, however, cannot weigh against so many other arguments. Miss Sykes' theory is grounded chiefly on an analogy with the Psilotaceæ, in which she regards the stalked synangium inserted on the upper surface of a lobed bract or leaf, as cauline; but it will be shown later that the balance of evidence is against this view.

But while agreeing with Dr. Scott's view that the sporangiophores represent lobes of the sporophyll, the present writer cannot adopt his conclusion that the fertility of the dorsal segments is a secondary modification. According to the theory of homologous

alternation pre-existing vegetative parts became in the phylogeny sporangiferous; but even the staunchest defender of the homologous origin of the sporophyte may well hesitate to assert that such highly organized structures as the sterile lobes of the Sphenophyllaceous sporophyll became sporangiferous. Dr. Scott adduces as an analogy the sporangia "commonly present" (8) on the frond of *Botrychium*. Professor Bower repeats this comparison in his latest publication (4). To this analogy two objections may be made. In the first place it seems a slight over-statement to say that sporangia are commonly present on the frond (as opposed to the spike) of *Botrychium*. Professor Bower himself, after a perusal of the literature on the subject and an examination of numerous specimens at Kew and at the British Museum, came to the conclusion that *Botrychium lunaria* was the most variable species (2). But even of this species he says "... however, I should wish to emphasize again the fact that in *Botrychium lunaria*, as collected in any average locality, the large majority of specimens show the sterile frond to be *normally* sterile, and the fertile spike to be *normally* fertile; that even in this species which appears to be the most variable in this respect, the phenomena above referred to are exceptional, and are, in my opinion, to be classed as *abnormalities*; while in other species of the genus, especially in the large-leaved forms, they are, if existent at all, so rare that they are seldom or never represented in herbaria, or recorded in the books" (2). Dr. Scott himself points out that in *Botrychium* "... there is still a marked difference between the frond and the spike, whereas in *Sphenophyllum fertile*, so far as the material allows of a decision, the dorsal and ventral lobes appear to have been perfectly similar to one another, though, with better material some minor differences may possibly be detected" (8). If the sporangia on the usually sterile frond of *Botrychium* are abnormal the analogy with *Sphenophyllum fertile* loses in force, for though it has recently been argued that "sports"—or the sudden appearance of exceptional characters may be perpetuated, under natural conditions, in the descendants of the forms producing them, this is by no means proved (13), and though we know that sporangia may and do appear as abnormalities on normally sterile parts, yet there is no proof that they have, *in nature*, been retained by the descendants of these malformed plants. On the other hand highly organized plants often show sterilization of sporangiferous parts. In any case, there is at least a probability that, if the sporangia on the

frond of *Botrychium* are not mere abnormal sports, they are ancestral structures. The spike of *Botrychium* is probably best regarded as a branch of the frond, to which the sporangia are now usually restricted; but such dimorphism may well be secondary, and in the remote ancestors of *Botrychium*, both main branches of the frond may have been fertile,—a less specialized condition than dimorphism. In that case the sporangia on the usually sterile frond of *Botrychium* would not be fresh developments, as Dr. Scott supposes those borne by the dorsal sporangiophores of *Sphenophyllum fertile* to be, but reminiscences of a primitive state. As already pointed out the want of differentiation between dorsal and ventral lobes is an important indication of primitiveness; other indications of this are the absence or small amount of union of the sporophylls at their base, and the fact that this theory of the primitiveness of the *Sphenophyllum fertile* type of cone enables us to interpret the cones of the allied Equisetales more satisfactorily, both as regards their relation to one another, and to the Sphenophyllales. On the other hand the secondary growth of the axis of the cone of *Sphenophyllum fertile* seems to be an acquired character, and one that might well arise if, as Dr. Scott suggests, supernumerary sporangia were formed. Dr. Scott has ably defended his theory, grounding his defence chiefly on two facts. Firstly on the fact that *Sphenophyllum fertile* is isolated as regards the fertility of the dorsal segments, and that it would be rash to regard this exceptional character as primitive. Against this it may be urged that the detailed structure of the fructification is only known in a few species of the phylum, and the negative evidence drawn from the absence of fertile dorsal lobes in the Sphenophyllales is not therefore very strong. But Dr. Scott also relies on the dorsiventral lobing of the sporophyll as proving that the lower lobes originally had a protective function that had “from some cause or other become superfluous, perhaps because the fertile laminæ formed by themselves a sufficient envelope to the cone” (8). In our present ignorance of the conditions under which the Sphenophyllales lived we may as easily suppose that further protection became, for some unknown cause, advantageous and that this brought about the sterilization and modification into a bract-like structure of the lower sporangiophores.

In *Cheirostrobus* each sporangiophore bore four sporangia; in *Sphenophyllum majus* each sporangiophore (or perhaps sporophyll) bore four sporangia; in *Bowmanites Römeri* and *Sphenophyllum*

fertile there were two sporangia on each sporangiophore; while in *S. Dawsoni* each sporangiophore bore a single sporangium. In the ill-understood *S. trichomatosum* each leafy bract-like structure apparently bore a single sporangium. There is also considerable variety in the numerical proportion the ventral segments bear to the subtending dorsal ones. In *Sphenophyllum fertile*, where both dorsal and ventral segments are sporangiophores, they are equal in number. This is so also in *Cheirostrobis*, in which the dorsal lobes are sterile bracts, and if reduced "sporangiophores" are present in *Sphenophyllum majus* and *S. trichomatosum* they are equal in number to the bracts, though unlike the latter they are undivided. In the types of *S. Dawsoni* and *Bowmanites Römeri*, however, the sporangiophores were twice as numerous as the dorsal lobes or bracts. If we accept, as the present writer feels compelled to do, Professor Lignier's derivation of the vegetative leaves of the Sphenophyllales from a smaller number of more highly compound leaves by the separation round the stem of the lobes of the compound leaves, we shall be tempted to regard the quadri-sporangiate sporangiophores of *Cheirostrobis*, associated with an equality in number of the dorsal and ventral lobes of the sporophyll, as primitive. In that case the type of cone primitive for the Sphenophyllales had sporophylls divided into an equal number of dorsal and ventral segments, all of which were sporangiferous and bore four sporangia. No cone combining these characters is known; but the occurrence of an equal number of dorsal and ventral segments in *Cheirostrobis*, the most ancient fructification of the Sphenophyllales known to us, and in *Sphenophyllum fertile*, which has been shown to be probably very primitive, marks out this character as a primitive one. That the quadri-sporangiate condition is also primitive appears very probable from its occurrence in a type so widely separated from *Cheirostrobis* as *Sphenophyllum majus*; this is further supported by the prevalence of quadrisporangiate sporangiophores in the older Equisetales; this is of importance, since it is now generally admitted that the Equisetales and Sphenophyllales had a common origin from strobiloid forms (6), (7), (9), (4). On this theory the type of *Sphenophyllum fertile* was evolved from the above hypothetical ancestor by reduction of the sporangia on each sporangiophore to two; in *Cheirostrobis* the sporangia were still formed in fours on the ventral segments, but the dorsal segments were converted into sterile bracts; it seems likely that in *Bow-*

manites Römeri there has been, accompanying the sterilization of the dorsal lobes, a fission of the ventral sporangiophores; this is borne out by the fact that in *Bowmanites* the sporangiophores are twice as numerous as the bracts, and that they bear two and not four sporangia. It would seem that in *Sphenophyllum Dawsoni* and the numerous allied cones this fission of the sporangiophore was accompanied by the reduction of the sporangia on each half (which then came to constitute a sporangiophore) to a single one. The origin of the type of *S. majus* and *S. trichomatosum* cannot be explained on this theory until their anatomy is known, but it is quite possible that in the former a sterilized dorsal lobe or bract subtends a much reduced sporangiophore bearing four sporangia; in this case the structure would be primitive in so far that the bracts and sporangiophores are equal in number, and the latter bear four (or more) sporangia. This reduction in number of the sporangia borne, on a sporangiophore, and the chorisis or fission of the latter, have been suggested by Professor Bower (3), but as he does not consider the sporangiophores and bracts as ultimately homologous, he would not, of course, accept the above interpretation of the homologies of the cones of the Sphenophyllales.

It is still doubtful whether all Sphenophyllales were homosporous; no undoubted case of heterospory has been discovered, though Mr. Thoday found a suggestion of it in *Sphenophyllum Dawsoni*, where there was a slight difference in size between the spores in certain sporangia, the larger spored sporangia occurring towards the base of the cone, where megasporangia are usually found (12). Dr. Scott subsequently expressed the opinion that heterospory is unknown in *Sphenophyllum*, although an appreciable difference in the size of the spores has been noted (9).

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II.—EQUISETALES.

THE first order contained in the phylum of the Equisetales, the Calamariae, consists only of fossils. The stems, marked externally with longitudinal ribs, show in transverse section a circle of woody bundles, separated by medullary rays and surrounding a pith. The remains of the protoxylem are distinguishable in a canal on the inner edge of each bundle, known as the carinal canal. The primary xylem was thus centrifugal, and beyond it secondary centrifugal xylem was also formed. Until 1901 it was generally thought that the xylem of Calamarian stems was wholly centrifugal, and that the protoxylem abutted on the pith; but in that year Dr. Scott described a stem to which he gave the name of *Calamites pettycurensis*, in which there is a considerable amount of centripetal xylem between the carinal canal and the pith (13). Owing to the fragmentary condition of the fossil it has been impossible to ascertain whether it belonged to *Archaeocalamites* or *Calamites*. Its discoverer considers its structure as primitive; the principal reasons for such a supposition are that there is, as will be shown later, good evidence that the Equisetales had a common origin with the Sphenophyllales, that there is some evidence of their common origin with the Lycopodiales also, though at a more remote period, and that in these two phyla the primary xylem was probably primitively entirely or largely centripetal. The antiquity of the fossil (it comes from the Calcareous Sandstone, a series of rocks occurring at the very base of the Carboniferous system) favours Dr. Scott's view, which is also supported by Professor Bower (2) and which few, if any, botanists would dispute.

In *Archaeocalamites* the vascular bundles and therefore the ridges on the stem were superposed at the nodes; in *Calamites* they alternated. *Archaeocalamites* appears in the Mid-Devonian, and is most abundant in the Culm, dying out at the very base of the Coal Measures (9); *Calamites* appears to have attained its maximum development in the Middle and Upper Coal Measures (9). Thus the former genus appears to be, on the whole, more ancient than the latter, and it is probable that the course of the vascular bundles in *Calamites* arose by the modification of the type of course found in *Archaeocalamites*. This appears to be Professor Seward's view, as the

following quotation will show : " On the whole considering the age of *Archaeocalamites* and the few characters with which we are acquainted, it is probable that this genus is very closely related to the typical *Calamites*, and may be regarded as a type which is in the direct line of development of the more modern Calamite" (16) Professor Seward also quotes cases of irregular superposition in *Calamites* and irregular alternation in *Archaeocalamites*. As in Grand'Eury's Permian *Autophyllites* the ribs of the stem did not usually alternate there appears to be some variety in the course of the vascular bundles, probably indicating that the transition from superposed to alternating bundles took place fairly easily.

In *Archaeocalamites* the leaves were dichotomously divided and Professor Lignier seems to have proved that, as in the *Sphenophyllaceæ* the numerous simple leaves of *Calamites* represent the segments of a smaller number of compound leaves (8). Dr. Scott has fallen in with this suggestion (15). The process of multiplication by precocious division of the trace within the tissues of the stem seems to have been carried further in *Calamites* than in *Sphenophyllum*, for the leaves are very numerous and uni-nerved; this might lead us to suppose that they represent ultimate pinnules. In *Autophyllites* we have a stage which is perhaps intermediate between *Archaeocalamites* and *Calamites*, for the leaves are once forked at their apex only. Owing to the great increase in the number of the leaves the numerical proportions were probably lost. We may still, however, see a trace of this origin by division of a smaller number of leaves and their vascular supply, for in the axes of the cones of some species of *Calamostachys* and *Palæostachya* (genera founded on Calamarian cones) though the members of each whorl are equi-distant their bundles are still grouped in pairs round the cauline stele, thus suggesting the origin of the numerous members of a whorl by the sub-division of a smaller number. The reproductive axis would then be more primitive than the vegetative one.

Leaving aside for the present the consideration of the cones of the Calamariæ, we will briefly consider the vegetative features of the Equisetaceæ. As here understood this order cannot be asserted to be a natural one, for it includes the two fossil genera, *Phyllothea* and *Schizoneura*, known only as impressions, whose position in the phylum it is difficult to estimate justly. *Equisetites* is also only known in impressions, but its similarity to *Equisetum* leaves no doubt of its close affinity with that genus. The stem of *Equisetum* contains a ring of collateral vascular bundles surrounding a pith. The most striking anatomical differences found within the genus

are connected with the distribution of the endodermis. These differences in the distribution of the endodermis have been clearly summarized by Sadebeck (11). Without entering into the morphological value of this layer it seems probable that the most primitive condition is that in which it forms a single ring surrounding the bundles. This is rendered probable by the fact that this condition is more widely spread than the others, and that no separate or internal endodermes are known in the Calamariæ, from which, as will be shown presently, the Equisetaceæ are probably descended. It also seems likely that the forms with an endodermis round each bundle (the so-called schizostelic or astelic types), and those with an internal endodermis, arose independently of one another from the normal type.

Conflicting theories have been brought forward concerning the nature of the vascular bundle of *Equisetum*; this consists of a median and two lateral portions. Long ago Strasburger put forward the view that these three strands represented the coalescent remains of three bundles. Dr. Scott, however, in a Course of Lectures delivered at University College in 1904, stated that he considered it clear that this was not so, because the protoxylem of the "bundle" was single and continuous throughout the longitudinal course of each bundle. Mr. Gwynne-Vaughan pointed out, in 1901, that only the median portion of the bundle, which contains the protoxylem passed out at the node as a leaf-trace; he also showed that the lateral strands had a different course from the median one; in the internode they lie "on adjacent sides of two different bundles" (4); they again approach one another at the node above, and in the next internode they occur in the same bundle. The same botanist remarks that the lateral strands do not appear to be a continuation of the centrifugal development of the median strands, but appear to be developed centripetally. This, however, could not be definitely proved, as no incompletely differentiated portions of the stem were available. Mr. Gwynne-Vaughan suggests that they are the remnants of a primitive mass of xylem, pointing out that this would be in complete agreement with their apparently centripetal development and cauline course. Another argument in favour of their representing primary centripetal xylem is that of exclusion. If they are not the vestiges of primary centripetal xylem, they must be the remains of two other endarch bundles, as suggested by Strasburger; or the remains of secondary xylem; or fresh developments of the individual bundles. The first of these possibilities is to a great extent barred by the fact that these lateral strands not

only appear to be centripetal, but that they have no protoxylems and therefore show no signs of fascicular individuality. The third suggestion, namely that these lateral strands represent a fresh development, is untenable in view of the conclusive evidence that the Equisetaceæ have in the course of their evolution undergone considerable and continuous reduction. It therefore seems that they must either represent reduced secondary xylem, as suggested by Dr. Scott, or reduced centripetal primary xylem as contended by Mr. Gwynne-Vaughan and Professor Bower (4) (2). Against the former alternative it may be urged that the development of these lateral strands appears to be centripetal; that Mr. Cormack has discovered what he considers to be secondary thickening at the node of *Equisetum maximum* (3) and that this thickening appears to be unconnected with the lateral strands; but this so-called secondary thickening is compared to the nodal thickening of a Calamite, and as Dr. Scott pointed out, in the course of lectures previously referred to, it has not been proved that this nodal thickening of *Calamites* was a secondary growth. If, however, Dr. Scott is right in regarding these lateral strands as reduced secondary xylem their lateral position is unintelligible, as secondary xylem naturally arises at the periphery of the primary xylem. Against the view that the lateral strands represent primary centripetal xylem it may be pointed out that these lateral strands do not occur in any of the numerous and well-preserved Calamariæ; as these plants are probably very close to if not actually on the direct line of descent of the Equisetaceæ, we should expect that, if the lateral strands represent vestigial centripetal xylem, they would be at least equally well represented in them. Further, centripetal xylem is only known among the Calamariæ in *Calamites pettycurensis*, where it occurs on the inner edge and not at the sides of the carinal canal. But the whole of the axis within the carinal canal was presumably at one time in the history of the race occupied by centripetal xylem, *i.e.*, the Equisetales probably had protostelic ancestors. The reduction of the centripetal xylem, reduced to an arc in *C. pettycurensis*, was probably brought about by the development of centrifugal xylem, which, as observed by Dr. Scott, frequently encroaches upon centripetal xylem (14). As the development of the median strands commences from a median point, and as they are wedge-shaped, it may well be that the arc of centripetal xylem, present in *C. pettycurensis*, was split by encroachment of the centrifugal xylem and that this process resulted in the lateral, apparently centripetal strands of the Equisetaceous bundle. On the whole, however, the

question of the nature of the lateral strands in the bundle of *Equisetum* must be left open.

In *Schizoneura* and *Phyllothea*, two fossil genera from the Upper Palæozoic and Lower Mesozoic beds, the ribs on the stem do not alternate at the nodes, whereas this alternation is the rule in *Equisetites* and *Equisetum*. For reasons given when discussing the the Calamariæ there can be little doubt that the latter condition was evolved from the former.

In *Phyllothea* the leaves of a whorl, though connected at their base, had free spreading limbs. The leaves of *Equisetites* and *Equisetum* are united into a sheath at the base, from which their apices only project as small teeth. This condition probably arose from such a one as found in *Phyllothea* by the reduction of the free portions of the leaves. In *Schizoneura* the leaves are united into a long sheath with small projecting teeth, the sheath being split into two or more broad lobes. This condition may have arisen by the greater development of the sheath from a type of leaf like that of *Equisetum*, in which the free portions of the leaves were already much reduced, or more probably by the extension upwards of the basal fusion of the leaves of such a type as *Phyllothea*.

The strobili of the Equisetales are extremely varied. In *Archæocalamites* the cone consists only of superposed whorls of sporangiophores; in the recent *Equisetum* the cone normally consists of alternating whorls of sporangiophores; in the fossil *Pothocites*, known only in impressions, the fertile whorls appear to be superposed and interrupted at intervals by whorls of leafy bracts; in *Calamostachys* equi-distant sterile and fertile whorls succeed one another on the axis of the cone, the former alternate with one another and consist of twice as many members as the latter, which are said to be superposed to one another. In *Palæostachya*, fertile and sterile whorls consist of an equal number of members and are superposed to one another, the sporangiophores being inserted just above the bracts. In *Calamostachys* the vascular supply for the bract and the sporangiophore above it originate according to Renault (quoted by Dr. Scott in the course of lectures already referred to) at the same place on the stele, namely at the insertion of the bract. Mr. Hickling has shown that this is so also in *Palæostachya*. It might appear natural to those who admit the affinity of the Equisetales and Sphenophyllales and who regard the sporangiophores of the latter phylum as lobes of the sporophyll of which the dorsal lobes are (except in *S. fertile*) sterile bracts, to look upon *Calamostachys* as a form derived from *Palæostachya* by the shifting upwards of the

ventral lobes or sporangiophores; but the course of the vascular strands as traced by Mr. Hickling forbids this assumption, for though their vascular strands originate at the same point as those of the bracts, they first ascend half-way up the internode and are then reflexed and follow a downward course, finally entering the sporangiophores just above their own point of origin (5). This behaviour seems to show that the approximation of the fertile and sterile whorls in *Palæostachya* is secondary and that this type of cone arose from a type in which as in *Calamostachys* fertile and sterile whorls were equi-distant from one another; indeed Mr. Hickling shows that the traces of the sporangiophores are slightly reflexed in a species of *Calamostachys*, described by Renault as *Calamodendrostachys Zeilleri* (5). It might at first sight appear as if Miss Sykes were correct in regarding the position of the sporangiophores on the axis as primitive, and in looking upon their frequent approximation to the bracts as secondary, since the sporangiophores are borne on the axis in *Archaeocalamites*, *Pothocites* and *Calamostachys*, and since their approximation to the bracts has been shown to be secondary in *Palæostachya*. It might also be used by Professor Bower to support his theory of the independence of, and the absence of homology between, bracts and sporangiophores (1). But both these writers, in common with the majority of recent botanists, admit the affinity of the Equisetales with the Sphenophyllales, and on neither of their theories can a satisfactory explanation be given of the structure of *Sphenophyllum fertile*. It is therefore preferable to regard the position of the sporangiophores on the axis, and their apparent independence of the bracts, as due to their displacement; this is strongly supported by the origin of the bract- and sporangiophore-trace at the same point on the cauline stele, and by the fact that shifting of the sporangiophore may clearly occur, since it has occurred in *Palæostachya*; this view is further borne out by the fact that, as Dr. Scott points out, characteristic nodal structure is confined to the insertion of the bracts. As regards *Archaeocalamites* we can hardly escape the conviction that its sporangiophores are the homologues of those of *Calamostachys*; and if so they are not phylogenetically speaking entire sporophylls, but lobes of sporophylls that have been separated from one another over the internode. In this case both dorsal and ventral lobes are fertile and this is probably a primitive character. It might of course be said that in *Archaeocalamites* the sterile bracts had become fertile; but the same very strong objections to this view explained in the case of *Sphenophyllum fertile* apply with

equal force here, and in this case they receive additional support from the extreme antiquity of *Archaeocalamites*. One might then explain the occasional sterile whorls of *Pothocites* (7) as being the first indication known to us of the sterilization of some of the lobes; in *Calamostachys* and *Palaeostachya* the dorsal lobes of the sporophylls are no longer sporangiophores, but have been sterilized. It is fair to add, however, that Graf Solms-Laubach considers that the cone of *Pothocites*, which is certainly ill-understood, has been misinterpreted (17). This derivation of a completely fertile cone from a type resembling *Sphenophyllum fertile* by the displacement of the upper lobe of a dorsiventrally divided sporophyll, of which both lobes were fertile, has been suggested by Dr. Scott, who applies the suggestion to the *Equisetum*-type (15); the types of *Equisetum* and *Archaeocalamites* are, however, identical in fundamental structure, and what applies to one probably applies to the other also. Nevertheless the writer has not been able to find any passage in which Dr. Scott affirms, or even suggests a homology between alternate whorls of the sporangiophores of *Archaeocalamites* and the sterile bracts of *Calamostachys*. Indeed if he regards the fertility of the dorsal segments of the sporophyll of *Sphenophyllum fertile* as a later modification he could hardly derive so ancient a form as *Archaeocalamites* from this type. Professor Jeffrey takes a somewhat different view, for though he suggests a dorsiventral lobing of the sporophyll in the ancestors of the Calamariæ, he gives two alternative ways of accounting for the absence of sterile whorls in cones of certain members of the phylum; (a) that the "sporangiophores" of completely fertile cones represent fused dorsal and ventral lobes and (b) that the sterile dorsal lobes have become obsolete (6). There is, as he himself points out, at present no evidence in support of either of these views; but since their publication the discovery of *Sphenophyllum fertile* has shown that the dorsal lobes of a sporophyll may be fertile, and as Dr. Jeffrey is seeking to derive the Equisetales from the Sphenophyllales it would seem natural for him to accept the explanation given here of the completely fertile cones. The writer considers that the occasional sterile whorls which are present in *Phyllothea* as in *Pothocites* may possibly be sterilized sporangiophores, which, with the loss of their reproductive functions, have acquired greater vegetative development. Both Potonié (10) and Professor Seward (16) have drawn attention to the similarity between an abnormal cone of *Equisetum*, figured by the former, in which sporangiophores occur below a sterile whorl, and a fructification of *Phyllothea*. Potonié states that this abnor-

mality is not exactly rare in *Equisetum*, and that the figure he gives of it shows very clearly the close relationship of *Equisetum* and *Phyllothea*; he characterises the phenomenon represented by this spike of *Equisetum* as probably atavistic (10). Mr. Seward mentions the resemblance pointed out by Potonié between *Phyllothea* and such an *Equisetum* and remarks that it suggests a partial reversion to a Calamitean type (16). From this it would seem that these authors incline to the view that the strobilus of *Equisetum* arose from a Calamitean type of cone; but they offer no explanation of the absence of fertility of the Calamitean bracts. The present writer is not inclined to attach much importance to an abnormality; it seems more probable that the ancestors of the recent *Equisetum* and the mesozoic *Equisetites* had cones of the Archaeocalamitean type; it is true that the latter genus is a very ancient one, but a somewhat similar type of strobilus seems to have characterized the Permian *Autophyllites*, and whether *Equisetites Hemingwayi* be rightly named or not it proves the existence of an *Equisetum*-like strobilus in the Carboniferous age, and may prove to be on or near the direct line of descent of the Equisetaceæ.

The strobilus of *Cingularia* remains to be discussed. In the absence of structural specimens Professor Lignier, who upholds the view that the sporangiophores of *Calamostachys* are the displaced ventral segments of the sporophylls, has suggested that in *Cingularia* this displacement has been carried further, and that the sporangiophores are the ventral segments of the sterile whorl below them and do not belong to the whorl to which they are approximated (8). Dr. Scott has recently stated that this may be so (15). But in view of the fact that in *Sphenophyllum fertile* both lobes of the sporophyll are fertile and that in the very ancient *Archaeocalamites* all the appendages of the cone appear to be fertile, it seems more probable that the sporangiophores of *Cingularia* are the dorsal lobes of dorsiventrally lobed sporophylls, both lobes of which were presumably originally fertile, and that the ventral lobes of these sporophylls have been sterilized. This is borne out by Dr. Scott's statement that, according to the latest observations, the sporangiophores appear to have been partially fused with the whorl of bracts above them, which would be improbable if they belonged to the whorl below (15). Professor Lignier sought on general anatomical grounds to harmonize the structure of the cone in *Cingularia* and the Sphenophyllales, and as *Sphenophyllum fertile* was at that time unknown he was obliged to regard the fertile members as ventral

lobes; but this obligation no longer exists and the theory suggested here seems more probable.

Professor Lignier has also attempted to explain the difference in number between the bracts and sporangiophores of *Calamostachys*. He supposes that in a form in which, as in *Palæostachya*, the sporangiophores or ventral segments are equal in number to the dorsal segments or bracts, the former became associated and fused together (8). Dr. Jeffrey takes a different view, pointing out that the bundles in the axis of the cone are equal in number to the sporangiophores, and that this fact taken in conjunction with the position of the bracts leads to the conclusion that "the pairs of sterile leaves, were really dichotomously divided segments of sporophylls, of which the sporangiophores were ventral segments" (6). This seems a more likely theory, in view of the fact that the sporangiophores of *Calamostachys* only bear the same number of sporangia as those of *Palæostachya*; if they were formed by the fusion of two of the latter we should expect them to bear more numerous sporangia.

Since dioecism may have prevailed in the Calamariæ it is impossible to prove that any given species is homosporous; but there is very strong negative evidence of their primitive homospory; indeed the heterospory of the *Calamites* is not of an extreme type. It is significant that neither in *Archæocalamites* nor in *Pothocites*, probably the two most ancient types, has more than one kind of spore been found; in some species of *Calamostachys* this is so too, though others have been proved to be heterosporous (12); further, the recent Equisetaceæ are homosporous and are obviously descended from homosporous Palæozoic Equisetales. Dr. Scott has shown that heterospory probably arose by the abortion of certain spores in order to facilitate the nutrition of the remainder (12). In that case it probably arose in more than one evolutionary series of the Calamariæ. Dr. Scott's suggestion that *Palæostachya* may have been heterosporous bears this out.

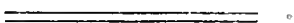
As regards the affinity of the two orders, they are evidently very closely related. Many botanists regard the Equisetaceæ as the direct descendants of the Calamariæ (12) (16). For as we pass upwards from the Palæozoic tree-like *Calamites* to the older of the Mesozoic *Equisetites*, which, though still very large were smaller than *Calamites*, and to the more recent species of *Equisetites* and finally to the living *Equisetum* we trace a steady diminution in size. Presumably some of the Mesozoic Equisetaceæ possessed secondary growth in thickness, for Professor Seward states that their rhizomes

may measure more than 12 cm. across and the sheaths on the aërial stem sometimes consist of as many as 120 teeth. In our living *Equiseta* no trace of secondary growth remains, unless the lateral wings of the bundles, or the nodal growth recorded by Mr. Cormack in *Equisetum maximum*, be a secondary growth (3). This is possible, but there is much doubt about the interpretation of both of these phenomena. This absence or reduction of secondary xylem, the reduction of its leaves, and its smaller size are the chief vegetative characters in which *Equisetum* differs from the *Calamariæ*. As regards the cone of *Equisetum* it is certainly far closer to the more ancient *Archaeocalamites* than to *Calamites*. For reasons already given the present writer finds it impossible to derive the cone of *Equisetum* from that of any known *Calamites*, but it is quite easy to derive it from the apparently completely fertile cone of *Archaeocalamites* by way of *Equisetites* and, possibly, of *Antophyllites*. On the other hand the ancestors of *Equisetum* presumably early acquired the simple leaves and the alternation of the bundles at the nodes characteristic of *Calamites*. As *Archaeocalamites* was probably very near to the line of descent of *Calamites*, the latter genus and *Equisetum* may have had a common ancestor with a cone like that of *Archaeocalamites* and *Equisetum*, but with the bundles of the vegetative and reproductive axes already alternating at the nodes; on the other hand this alternation may have been acquired independently in the ancestors of both genera. As regards *Schizoneura*, whose fructification is unknown, the superposition of the bundles at successive nodes warrants the supposition that it may have arisen from a type resembling *Archaeocalamites*. *Phyllothea* too, probably originated from an *Archaeocalamitean* type, possibly through a form like *Pothocites* by the sterilization and leafy development of occasional whorls of sporangiophores.

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NOTES FROM THE CAMBRIDGE BOTANY SCHOOL.



III.—ON A BRANCHED CONE OF *Equisetum maximum*, Lam.

[TEXT-FIGS 19, 20].

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SPECIMENS of *Equisetum* in which branching of the strobilus has taken place are not infrequently met with, and have been referred to by various writers from time to time.¹

In view of the possibility that such abnormal types of structure may shed some light on morphological problems, the structure of a cone of *E. maximum*, grown in the Cambridge Botanic Garden,

¹ Milde, J. Nova Act. Acad. Caes. Leop. Carol., Vol. XXVI., Part 2, p. 412, 1857. Duval-Jouve, J. Histoire Naturelle des *Equisetum* de France, p. 152, Paris, 1864. Lucrassen, C. in Rabenhorst's Kryptogamen-Flora III., p. 683, Leipzig, 1889.

and in which branching of the strobilus had occurred, was thought worth recording.

Before removal of the scale-leaves the strobilus in question appeared to be of normal size. On removal of the scales four smaller cones were found to arise slightly above the middle of the chief cone (Fig. 19, A and B).

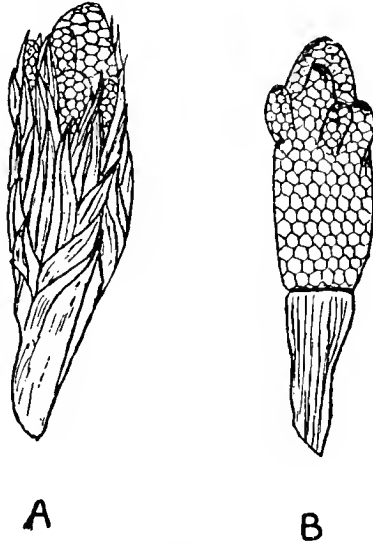


Fig. 19. Branched cone of *Equisetum maximum*. A.—Before removal of scales. B.—After removal of scales. $\times \frac{4}{5}$

The internal structure of the single specimen was investigated by means of transverse sections only. As stated by Professor Bower,¹ the method of branching of the strobilus is fundamentally dichotomous and quite different from that exhibited in the formation of lateral branches. In this cone the stele of one of the side branches is nearly of the same size as that of the main axis, the other three branches being much smaller.

At the base of the cone the structure is of the normal type. The first sign of bifurcation of the axis is a broadening of the stele in one direction. The broadened stele then becomes constricted at a point on the longer diameter. The two parts of the stele on either side of this point then become more and more cylindrical by the closing together of opposite sides of the stele at the constriction. Finally, the two cylinders close up so that each branch of the bifurcation has its own stele.

The most interesting feature of the cone is the presence of vascular bundles in the pith of the main axis. These bundles end blindly in the downward as well as in the upward direction, but shew a tendency to branch among themselves. They are quite unconnected with the ring of normal vascular tissue. The number of bundles in any one transverse section never exceeds three, and

¹ Bower. *Origin of a Land Flora*, p. 682, London, 1908.

these appear to be arranged as portions of a ring as indicated in Fig. 20 A.

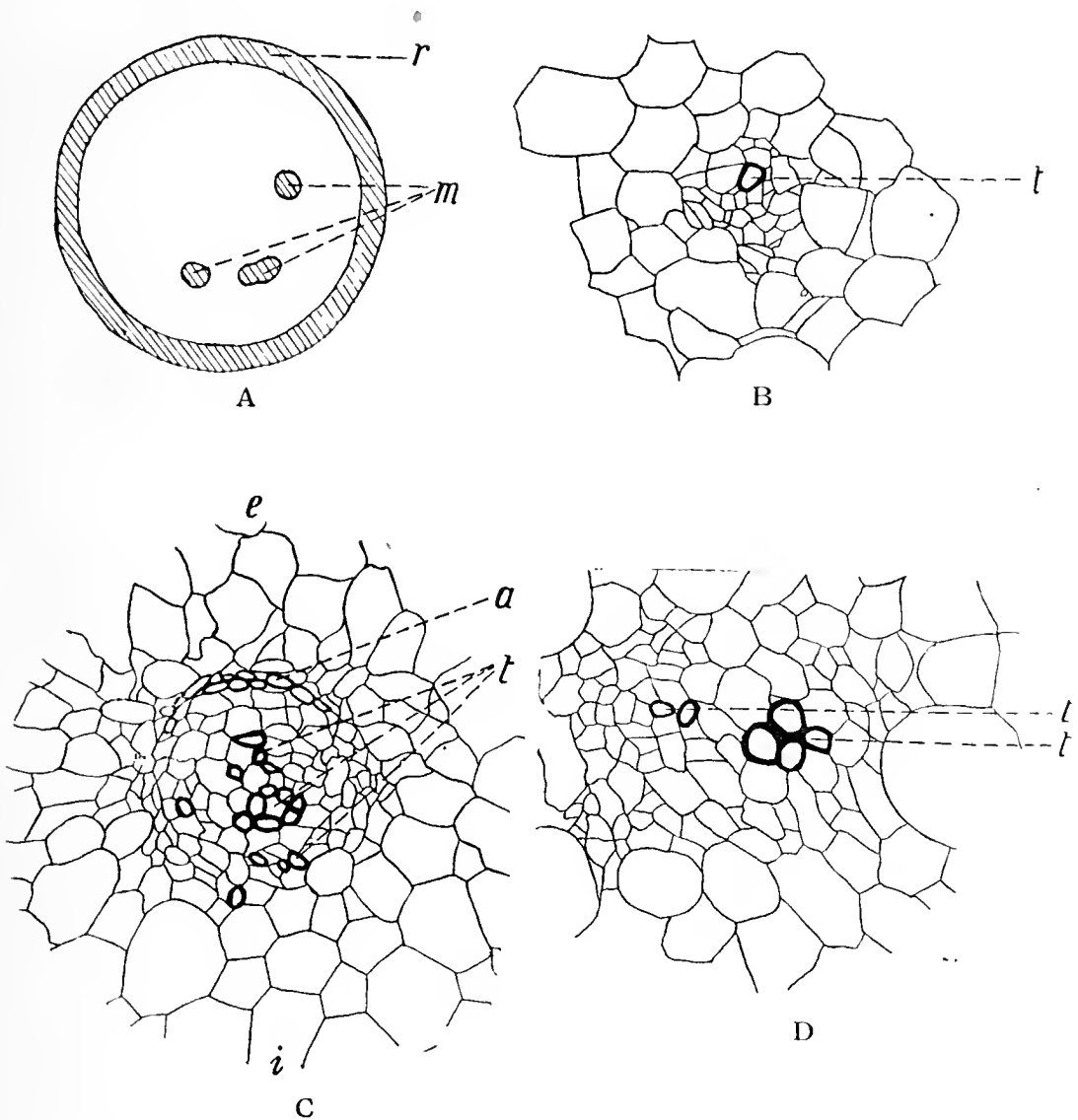


Fig. 20. A, Diagram shewing the position of the medullary strands. *r*, normal ring of bundles; *m*, medullary strands; B, C, D, Transverse sections of bundles in the pith. $\times 100$. *e*, side of the bundle towards the periphery of the cone; *i*, side of the bundle towards the centre of the cone; *t*, tracheids; *a*, thick-walled parenchymatous cells on the outside of some of the bundles.

Fig. 20c shews the appearance usually presented by these medullary bundles in transverse section. They are generally more or less circular and consist of a few tracheids (Fig. 20c, *t*) scattered irregularly among small-celled parenchyma. On the inner side they pass gradually into the ground-tissue of the pith, but the side towards the periphery of the stem is generally bordered by some thick-walled parenchymatous cells (Fig. 20c, *a*). No evident phloem could be made out.

Fig. 20B shews a section of a bundle near its uppermost limit. Fig. 20D represents a section of a bundle just before dying out in the downward direction.

At the British Association meeting of 1901, Mr. Gwynne-Vaughan¹ shewed that the so-called vascular bundle of *Equisetum* consists of three strands; a carinal strand, part of which passes out as a leaf-trace, and two lateral cauline strands. He also found that whereas the xylem of the carinal strand is mostly or wholly centrifugal in its development, that of the lateral strands shews indications of having been formed centripetally. He came to the conclusion that the stele of *Equisetum* was in all probability originally protostelic and that the lateral cauline strands represent the remnants of a former large development of centripetal wood. The discovery made by Dr. Scott,² announced at the same meeting, of centripetal wood in the stem of *Calamites pettycurensis* lent support to this view.

It is perhaps possible, as Professor Seward suggested to me, that the bundles in the pith of the branched cone of *Equisetum* may be the remnants of the solid central stele of the ancestors of the living species of *Equisetum*. Since these bundles are quite unconnected with the normal ring of vascular tissue they are evidently not formed by the branching of normal strands. Moreover, their structure is different from that of the normal bundle, their resemblance being rather to a simple protostele than to anything else.

Having regard to these two facts, together with the probable absence of phloem from the medullary vascular strands, and bearing in mind that it is in the reproductive parts of plants that pre-existing structures are likely to occur, it would seem quite possible that the medullary strands in question are the remains of a primitive solid central mass of centripetal xylem.

¹ Gwynne-Vaughan. Brit. Ass. Rep., 1901; *Annals of Botany*, Vol. XV., p. 774, 1901. See also Bower, *Origin of a Land Flora*, p. 388, 1908.

² Scott. Brit. Ass. Rep., 1901; *Annals of Botany*, Vol. XV., p. 773, 1901.

PROFESSOR BOWER ON THE THEORY OF ANTITHETIC ALTERNATION OF GENERATIONS.¹

BRITISH plant-morphologists, especially those who interest themselves in that striking phenomenon which characterises the life-histories of a great portion of the vegetable kingdom, the regular alternation of sexual and asexual generations, have been expecting the publication of the present work with great interest. Professor Bower's name, perhaps more than that of any other botanist, is identified with research into the morphological problems connected with this great and still incompletely understood phenomenon of plant-life. It is to him, more than to any other, that we owe the great revival of interest in these problems which took place in this country about twenty years ago; it is to him that we owe the stately series of memoirs embodying a very large portion of our detailed knowledge of the structure and development of the "spore-producing members" of the Pteridophytes, investigations undertaken with a view to elucidating certain aspects of the general problem; and it is very largely to the stimulus of his enthusiastic example that we owe the general accumulation of researches—largely British—on the structure and development of the Archegoniatae which have made this group to-day one of the most completely investigated in the plant-kingdom.

The debt that morphologists owe to Professor Bower is therefore no inconsiderable one, and the publication of his matured conclusions—the results of the thought and research of half a life-time—is naturally an occasion that calls forth our gratitude no less than our interest.

The main thesis of the book before us is the same which the author put forward nearly eighteen years ago in a paper "On antithetic as distinct from homologous alternation of generations," published in the fourth volume of the *Annals of Botany*. In that paper, as Professor Bower says in the preface to the present work, "the main position of Celakovsky in discriminating between Homologous and Antithetic Alternation was adopted; but the latter type, as seen in Archegoniate Plants, was recognised as having been fixed and perpetuated in accordance with the adaptation of aquatic organisms to a Land Habit." The essence of this theory is that not only the sporogonium or fruit-body of the Bryophytes, but also the sporophyte or leafy plant of the Pteridophytes has arisen as a new intercalated phase in the life-history of a hypothetical gametophytic ancestor which did not possess such a phase, by gradual elaboration of the oospore or fertilised egg.

Recognising that the morphological and developmental facts were at that time much too inadequately known to allow of a full and reasoned statement of this theory, Professor Bower undertook the series of "Studies in the morphology of spore-producing members" to which we have already alluded, and on the completion of these in 1903 at length found himself in a position to put forward

¹ The Origin of a Land Flora, a Theory based upon the facts of Alternation, by F. O. Bower, Sc.D., F.R.S., Regius Professor of Botany in the University of Glasgow. Pp. XII. and 727. 361 Figures in the Text. London, Macmillan & Co., 1908. Price 18/- net.

the detailed statement of the phenomena involved which is presented in the present work.

The method adopted is to begin with a "Statement of the Working Hypothesis" (Part I.) which occupies no less than 254 pages; then to give a "Detailed Statement of Facts" of the development, structure and relationships of the different types of Archegoniate sporophyte (Part II., 402 pages); and finally to present a summarised "Conclusion" (Part III., 109 pages).

After a short introduction, setting forth the general theory, in which all botanists will agree, that the main progress of evolution within the plant-kingdom is a gradual and progressive adaptation to terrestrial life, Professor Bower contributes a thoughtful chapter on the "Scope and Limitations of Comparative Morphology," and then proceeds, by gradual steps, to come to close quarters with his "working hypothesis." After setting out the leading facts of the alternation of generations as seen in the life-history of a fern and discussing the "balance" of the two generations in the different groups of Archegoniataë, he deals in two useful chapters with the cytological distinction between the generations (including a discussion of the extremely important recent work of Farmer and his collaborators on the cytology of apospory and apogamy) and with the varied and complicated phenomena of alternation seen in the Thallophyta. The author's treatment of this last subject is particularly able and acute.

Professor Bower next proceeds to discuss "the biological aspects of alternation," restating the theory embodied in his paper already referred to. Admirably worked out as that theory has been by the author, it is, however, not quite legitimate to *identify* the "biological" theory of alternation with the "antithetic" theory, as is apparently done on p. 86. No one doubts that the factors of increased spore-production, of the appearance of typical land-roots, of a differentiated conducting system, and of the general elaboration of the sporophyte, have been the important factors in adapting the sporophytes of vascular plants to a terrestrial existence. What is doubted is the evolution of this sporophyte from a body of spores produced by the segmentation of the zygote; and it is quite possible to derive the terrestrial sporophyte, with its gradually increasing adaptation to drier conditions, from a spore-bearing thallus. The "biological theory of alternation," so far as it concerns the Pteridophytes themselves, does not, then, necessarily rest upon an "antithetic" basis.

In his next chapter Professor Bower deals with "Sterilisation," *i.e.* the conversion, in the course of descent, of sporogenous into vegetative tissue. The actual existence of this process is amply demonstrated in a varied series of instances, and the contention of the author "that plants show not uncommonly to-day such a conversion of cells from the propagative to the vegetative state as the antithetic theory would demand" is fully borne out. In his three chapters dealing with sporangia, the author presents most valuable analyses of the nature of these organs and their relations to the vegetative development of the plant as a whole.

With the eleventh chapter, "The Theory of the Strobilus," we come to the central point of Professor Bower's hypothesis, and it is here, naturally enough, that those who have come to other conclusions as to the probable ancestral history of the Pteridophytic

sporophyte, will find a good deal with which they must disagree. Professor Bower's view is that in the "strobilus" or fertile sporangium-bearing spike characteristic of the small-leaved groups of Pteridophytes (the Club-mosses, Horse-tails and Sphenophylls) we have the prototype of the leafy sporophyte, and at the same time the point of contact with the Bryophytic sporangium. This is of course the crucial question, and goes to the root of our whole conception of the morphological construction of the leafy plant-body.

After contending, quite properly, that "we have no right to assume that the leaf was formed once for all in the descent of the sporophyte" the author states three possible views of the origin of a foliar differentiation of the shoot in vascular sporophytes: "(1) That the prototype of the leaf was of prior existence, the axis being a part which gradually asserted itself as a basis for the insertion of those appendages (2) That the axis and leaf are the result of differentiation of an indifferent branch-system, of which the limbs were originally all alike . . . (3) That the axis pre-existed, and the foliar appendages arose as outgrowths upon it."

The first of these views, the so-called "phyton-theory" proper, at least in Celakovsky's most recent expression, is based on the assumption (not at all a necessary assumption, as Professor Bower remarks) that there must exist in the plant-body morphological entities intermediate between leaf-bearing shoots on the one hand, and cells on the other. These intermediate entities Celakovsky found in his *Sprossglieder*, each *Sprossglied* being a leaf together with its stem-segment. From the point of view of evolutionary morphology such a theory can only have a real meaning if we suppose the body of a vascular plant to have arisen by the superposition of successive leaves, or the prototypes of leaves, each of which springs from its predecessor. Such a supposition would carry with it the consequence that the axis or stem is entirely secondary in origin. But an origin of this kind is not supported by evidence from the lower plants. The assimilating thallus, whether dorsiventrally or radially organised, found in many Algae and Liverworts, represents the material, so to speak, out of which both leaf and axis can be differentiated. It is no more reasonable to regard it as the prototype of the leaf alone than of the axis alone. Thus the "Sprossglied" must be regarded as an entity which is ideally constructed and has no existence as an objective morphological phenomenon.

"The second view, that the axis and leaf are the result of differentiation of an indifferent branch-system of which the limbs were originally all alike, has lately been brought into prominence by Potonié," though it was suggested years ago by Professor Bower himself, and, as he remarks, both Hallier and Lignier have put forward similar theories, while the reviewer has recently expressed the opinion that "a strong case has been made out" for the hypothesis.

Our author's objections to this view are as follows. First he questions whether "such an origin is in any way applicable to the Lycopods, Equiseta and Sphenophylls," *i.e.* to the typically microphyllous forms in which each individual leaf is at present at any rate, both by development and position, quite obviously a comparatively small lateral appendage to a radially organised axis. Secondly he points out that "in their individual

development all sporophytes are originally radial, a condition which has probably a very close relation to their production in the archegonium"; consequently he objects to a theory which would make the dorsiventral condition primitive, and the radial derived, as has been done in the form of this view recently maintained by the authors quoted. Finally he remarks that "there is no known case of dichotomy in the sporophyte, where one branch develops as axis and the other as leaf."

It cannot be denied that the first two objections have considerable force. No one, certainly, would set out to explain the origin of the leaves of the microphyllous Pteridophytes, if these were the only forms known to us, as derived from branches of a dichotomous thallus of which the sister branches represented in each case the continuation of the axis beyond the insertion of the leaf. Nor can it be denied that the radial organisation of the young Pteridophyte is a strong, though not perhaps a conclusive, piece of evidence for regarding this type of organisation as primitive in the group.

The third objection, that we never in fact get a case of "dichotomy" in which one branch becomes a leaf and the other an axis, will not however bear analysis. For what is the test of such a "dichotomy"? Certainly not an equal symmetrical division of an apical cell or multicellular meristem, for *Dictyota* is practically the only known case in which such an equal division occurs. In practice, branching is said to be dichotomous when an elongated organ produces two branches of the same morphological nature and of approximately equal strength, neither of which *appears* to be a direct continuation of the original axis. Such branching may arise, so far as we know, in two different ways. In one case, found among Liverworts, the original apical cell or cell-group stops growing, and two new growing points are initiated right and left of it. In the other a new apical cell is initiated in a segment or the product of a segment of the original apical cell (which continues to divide), but the branch thus laterally produced grows as vigorously as the continuation of the original axis and a "dichotomy" is the result. Now there is no essential histogenetic difference between this process and the origin of a fern-leaf close to the apex of the stem-axis. It is therefore quite illegitimate to argue that a theory of the origin of the leaf and stem of a fern from originally equivalent "dichotomous" branches is excluded because there is no dichotomy as between the leaf and stem of a fern, and it is meaningless to say that the theory "appears to break down on the test of fact." If the histogenetic criterion is to be applied, the plain result is that no such thing as strict dichotomy exists among plants at all except in *Dictyota* and some filamentous Thallophytes. The problem we are really concerned with is the question whether the precursors of stem and leaf are derived from branches, originally equivalent in nature, of a forking thallus. While it is certain that we have no direct evidence of such an origin, it may be fairly contended that it is perfectly practicable, and not inconsistent with anatomical evidence derived from the more primitive ferns.

If we use the word "dichotomous" as it is commonly applied, abandoning the histogenetic criterion, it becomes clear that the distinction between "monopodial" and "dichotomous" branching

is merely a difference of the direction and degree of development of the two branches, and we can pass from one to the other with great readiness. A comparison of two such forms as *Fucus* and *Halidrys* shows that a passage from an apparently more primitive equivalently branched "dichotomous" thallus to an apparently monopodial system, in which some of the lateral branches are differentiated, has actually occurred, and it is such a passage which is hypothecated by the theory under discussion. Direct evidence of such a change in the ancestors of the Pteridophytes is not available because such ancestors are unknown. The differentiation between the specifically assimilating and specifically supporting members is already fully established in the most primitive members of the Pteridophytic stocks. The "test of fact" is no more applicable to such a theory than to Professor Bower's "enation" theory of the origin of the leaf. If it were, the controversy would be at an end.

It may be admitted, however, that it is unnecessary to burden the theory of the origin of the leaf and stem from branches of originally equivalent morphological nature with any hypothesis of the primitiveness of "dichotomy," and Professor Bower's criticisms certainly help to bring this conclusion into relief. The real weakness of the theory of primitive dichotomy appears to the present writer to be the absence of evidence that is primitive among the Green Algæ, where clear monopodial branching of the thallus is extremely common, and the elaborateness of the hypotheses required to support a theory of the origin of the whole plant-body from a dichotomous thallus in the microphyllous Pteridophytes. To these considerations must be added Professor Bower's point about the primitively radial construction of the young sporophyte, even in Ferns.

If the primitive sporophyte were originally free-living it is conceivable that it was originally dorsiventral in structure and that the almost universal radial structure of the young sporophyte of the present day has been impressed upon it by its imprisonment within the archegonium. To such a view it may, however, be fairly objected that the hypothesis is gratuitous, without stronger evidence of primitive dorsiventrality than we actually possess.

We may more easily derive the microphyllous forms with whorled or spiral leaves from a radially organised thallus with monopodial branching, or with mixed monopodial and dichotomous branching. The exact stage at which the specialised assimilating leaf-structures were separated from the supporting axial structures it is, of course, impossible to determine. But it may be relevantly pointed out that among the Algæ there exist an abundance of types of branched thallus from which the various forms of morphological construction actually found among the Pteridophytes can be theoretically derived without any series of gratuitous assumptions. The fact that these types of thallus actually bear sexual organs as well as spores is not, of course, any obstacle from the standpoint of believers in the "homologous" theory of the origin of alternation.

From this somewhat lengthy discussion of the theory "that the axis and leaf are the result of differentiation of an indifferent branch-system of which the limbs were originally all alike," (a view which the reviewer still considers as the least open to objection if it is freed from the further hypothesis that this primitive branch-

system was always and exclusively dichotomous) we pass to a consideration of the "third view" (which is Professor Bower's own), "that the axis pre-existed, and the foliar appendages arose as outgrowths upon it."

It will of course be admitted by the author's opponents that a thallus-axis of some sort pre-existed among remote algal ancestors. The point in dispute is whether an axis without foliar appendages existed in the immediate ancestors of the Pteridophytes. From such an axis Professor Bower believes that leaves arose by "enation," *i.e.* by exogenous outgrowth from a previously vacant surface. We have to imagine an ancestral sporogonial axis without appendages. This, according to the author, became differentiated into a fertile upper region with the power of apical growth, and a vegetative base; the sporogenous cells were then relegated to a superficial position and segregated into separate pockets or sporangia; and finally there was enation of the foliar appendages. It also had to originate a root-system, whose mode of origin is left doubtful.

It may be freely admitted that this is a perfectly clear, clean-cut theory, which harmonises the Bryophytic sporogonium with the Pteridophytic sporophyte, and accords well with the cytological facts of chromosome reduction in the process of spore-formation throughout the Archegoniate series. It also accords with the general similarity of the Fern-prothallus and the Hepatic thallus, and of the archegonium in the two groups. Let us see what is the main evidence brought forward in its favour in the course of this eleventh chapter—"The Theory of the Strobilus."

Professor Bower remarks that "much of the difference of view as to foliar origin centres round the question whether originally the leaf was relatively large or small." In other words if we can establish a presumption that the small-leaved strobilate Pteridophytes are relatively primitive and the Ferns derived we shall reach a firmer basis for the sporogonium and enation hypothesis. On this point he cites anatomical evidence. Adopting Jeffrey's distinction of the cladosiphonic type in which the gaps in the stele are branch-gaps only, and the phyllosiphonic type, in which the stellar gaps are connected with both branches and leaves, Professor Bower states (p. 140) that "in certain Ferns the progression may be traced from the cladosiphonic in the young plant to the phyllosiphonic in the mature, thus suggesting a similar progression in descent, *viz*: that the large-leaved phyllosiphonic Ferns were derived from a smaller-leaved cladosiphonic stock." The reviewer is unaware of any case in which the stele of a young fern shows branch-gaps and not leaf-gaps. The cladosiphonic and phyllosiphonic types of structure distinguished by Jeffrey are characteristic respectively of the microphyllous and megaphyllous phyla of Pteridophytes, *when the structure of the stem is siphonostelic*. To the *protostelic* types of any phylum it does not apply, because there cannot be leaf-gaps in protostelic forms. The ordinary progression seen in the young fern-stem, is from the protostelic to the siphonostelic condition. But protostelic forms are in no sense cladosiphonic, and afford no presumption whatever of derivation from a microphyllous type.

The leading argument used by Professor Bower in this chapter may perhaps be fairly stated as follows: that there is a presumption in favour of the origin of foliar appendages by enation because

“the appendages actually appear in the ontogeny by enation” (p. 141). This argument is stated several times, and is evidently regarded as of primary importance. It is really difficult to know how to meet such a contention except by a blank refusal to accept the validity of so crude an application of the facts of ontogeny to the elucidation of a phylogenetic problem. We had supposed that modern morphologists had agreed to abandon this kind of method altogether. Let us see where it would lead us in the first case that comes to mind. The sporangia of Leptosporangiate Ferns undoubtedly “appear in the ontogeny by enation.” Would Professor Bower therefore conclude that that was their origin in evolution, or even that the ontogenetic fact afforded any presumption in such a direction? We know, on the contrary, that he regards this particular type of sporangium as having had a long ancestral history, and as ultimately derivable from a portion of the continuous sporogenous layer of a Bryophytic sporogonium. Similarly the opponents of the “enation” theory of the phylogenetic origin of the leaf believe that the leaves of Pteridophytes originated from pre-existent structures, and cannot possibly accept their ontogenetic origin by enation as affording any presumption to the contrary.

At the close of the chapter (p. 143) the author appears in the character of an innocent person unjustly accused of making “tremendous morphological assumptions in the way of the origin of new organs.” His defence is that “the only assumption apparent to the mind of its author [*i.e.*, of the strobiloid theory], is that the order and mode of origin of the appendicular parts in the course of Descent has been that which is actually seen in their individual development.” Instructive light is thrown on the plea that such an assumption is justifiable by a statement which appears on p. 152 in another connexion. “It is often assumed” says Professor Bower, “that the vegetative leaf was pre-existent in descent to the appendages of the strobilus, *the mind naturally translating the successive events of the individual life directly into the history of its evolutionary organisation*” (italics ours), and he goes on to show that such an assumption is illegitimate. The author here, and in other similar passages, directly contributes to his own conviction on the charge of making assumptions, which he himself appears to recognise as illegitimate, and which it is scarcely unfair to describe as “tremendous.”

We think that the readers of a work of the size and scope of Professor Bower's book, into which the controversial element necessarily enters to a large extent, have good reason to complain that the author has not devoted a great deal more time and space to considering the objections to his theory. These objections may be roughly classed as “general” and “special.” Of the former we may distinguish the following:—

(1.) It is *a priori* in the highest degree unlikely that so fundamentally important an organ as the foliage leaf of the vascular plant appeared in descent as an “enation” from the surface of a cylindrical body of different morphological nature. There is no well-established case of any such origin of an organ of the importance and with the potentialities of the leaf in the evolutionary history of the plant-kingdom. That enation of hairs and prickles has frequently occurred is true; but the potentiality of

development of such structures, as judged by their subsequent evolution, is quite insignificant in relation to the plant-body as a whole. We cannot so lightly dismiss the instinct of our predecessors, who placed "emergences" in a morphological category quite distinct from leaves and stems.

(2). The apparently complete incapacity of any known Bryophytic sporogonium to produce by enation or otherwise anything in the nature of a foliage leaf or sporophyll, though both its spore-producing and distributing, and its assimilating mechanisms are frequently very highly developed, strongly suggests that the elaboration of the sporogonial fruit-body which we actually see represents its highest capacity of evolution; that it does not possess the morphological potentialities of an autonomous plant-body, and therefore cannot be regarded as the starting point of the vascular sporophyte.

(3). The branching thallus, on the other hand, as found among the Algæ and Liverworts, with its unlimited potentialities of apical growth, only conditioned by its facilities for the absorption and conduction of food, its mixed and often not sharply distinguishable dichotomous and monopodial branching, its lateral members with their variable specialisation for the assimilating function, undoubtedly furnishes a natural and practicable starting point for the development of the Vascular plants as we actually see them. The fact that the Vascular plant-body is always a sporophyte, while the Thallophyte plant-body has the capacity to produce both gametes and spores is, of course, to be correlated with the adaptation of the former to terrestrial life. The exact method of origin of the Vascular sporophyte from the ancestral Thallophyte cannot be determined on the morphological data available, but such an origin presents no insuperable theoretical difficulty in the light of modern work on the point of occurrence in the life-history of the reduction-division.

Of more special objections to the "strobiloid theory" the following may be cited:—

(1). The "strobiloid theory" requires the microphyllous Pteridophytes to be the relatively primitive forms, and the Ferns to be derived forms. While it is true that the microphyllous stocks are very old, there is no evidence that they are older than the Ferns. Further, dichotomous branching of the leaf is found among the oldest "microphyllous" forms, except in the case of the Lycopods, and suggests that evolution among these stocks has been from a larger to a smaller leaf in relation to the size of the stem.

(2). There is no evidence whatever among the oldest Ferns we know of any approach to the microphyllous type. Relative microphyly in the Fern-stock and its derivatives is clearly a reduction-phenomenon.

(3). There is no good evidence of any transition from the microphyllous stocks to the Fern-stocks. Lignier's speculations on the Filicinean origin of the Sphenophyllales and Equisetales, if they are to be accepted (which the reviewer is not inclined to assert), point to an evolutionary transition in a contrary sense. The Ophioglossales combine megaphylly with a position of the spore-bearing organs characteristic of the microphyllous types, and might be regarded as an ascending series from an ancestral micro-

phyllous stock. But they might equally be regarded as an isolated remnant of an ancestral megaphyllous stock with the adaxial position of the spore-bearing organs, from which the present microphyllous forms have been derived by reduction. The existence of relatively large-leaved ancient forms of Sphenophyllales and Equisetales supports the latter view. In any case the Ophioglossales do not represent a transition from microphyllous forms to the Ferns.

(4). On the general point of the relation of the "microphyll" to the "megaphyll," there is no evidence of any capacity of the microphyll to evolve into the megaphyll. The former seems to be most naturally regarded as an organ which by reduction, or by its original nature, does not possess the potentiality of further evolution.

The space we have devoted to Professor Bower's "Theory of the Strobilus" and the considerations which it suggests must be justified by the fact that this theory is the keystone of the author's morphological arch, and upon its validity depends the main thesis of the work. We must now return to a consideration of his succeeding chapters.

In dealing with "Sporangiophores and Sporophylls" the author shows how the use of the non-committing word "sporangiophore" has become necessary in the light of modern knowledge of the variety of spore-bearing organs, all of which certainly cannot be reduced to the concept of the sporophyll. Professor Bower considers that the sporangiophore is simply a placental out-growth and is therefore an organ *sui generis* not to be homologised with any other type of member. In the course of the chapter the author has some very wise cautions against the practice, still too common, of reading conceptions derived from a study of higher forms into the structural features of lower ones.

The next chapter is concerned with an attempt to show that the foliage leaf is a sterilised sporophyll, in opposition to the old notion that the flower is a modified foliage shoot, a notion which clearly cannot be interpreted directly in terms of descent, because spore-bearing organs must have pre-existed. But apart from the strobiloid theory it is not at all necessary to bind ourselves to one of these alternatives. The ancestors of the Pteridophytes must certainly have regularly formed sporangia, but they need not necessarily have done so on all their axes, foliar organs or appendages, any more than a Thallophyte does at the present day. Given the potentiality of forming reproductive organs of a definite kind, it is certain from Klebs' work that the time and position of their formation is *primitively* mainly determined by external stimuli. Later on in the course of evolution it becomes practically independent of these stimuli, the morphogenic impulse depending almost entirely (as it always did partially) upon internal stimuli which in their turn depend upon the regular sequence of events in a definite ontogeny. The regularity with which the reproductive cells are formed in certain positions will therefore naturally vary according to the degree of definiteness attained by this sequence, and according to the completeness of the shifting of the governing stimuli from external to internal factors. Upset the normal ontogenetic sequence, by the removal of leaves and the like, and you will upset the normal period

of production of the reproductive cells. A conception of this kind would seem amply to cover the facts cited by Professor Bower, without any appeal to a definite evolutionary sterilisation of obligate sporophylls.

In a chapter on Embryology and the Theory of Recapitulation Professor Bower reviews the history of this subject and shows how largely we have been obliged to abandon the somewhat rigid ideas of the earlier plant-embryologists. Out of the wreck, the author has saved the general fact of the origin of the stem-axis near the point of intersection of the octant walls of the epibasal hemisphere of the Pteridophytic embryo, and this he considers a material fact in relation to the strobiloid theory, because that theory "contemplates the phyletic pre-existence of the axis." With the author's conclusions as to the secondary character of so-called "independent" roots and leaves and as to the true foliar nature of the "cotyledon" in Pteridophytes we are in close agreement.

The author next presses the Stelar Theory into the service of his hypothesis of the strobilus. He argues that "the existence of a cauline stele bears directly towards a strobiloid theory of the shoot," and brings in the example of the vascular cylinder of the Moss gametophyte as an instance of the existence of a stele independent of leaf-traces, connecting this with the state of things existing in the microphyllous Pteridophytes. We may all agree that the anatomical structure of Pteridophytes lends no support to a phytonic theory, and that it is *consistent*, so far as the microphyllous forms are concerned, with the strobiloid theory. But it is just as consistent with the theory of origin of the sporophyte from a branching thallus. And when Professor Bower asserts, as he does in one of his headlines (p. 199) that the anatomical evidence "shows microphylls to be primitive" we must take leave to differ from him completely. The argument here is based on an apparent confusion, already alluded to, of a condition of protostely with cladosiphonic siphonostely. Mr. Gwynne-Vaughan will probably be surprised to learn that he has shown a "transition from the cladosiphonic to the phyllosiphonic" state in the young plant of *Alsophila excelsa*. What really exists, of course, is a transition from protostely to siphonostely, and protostely is not a monopoly of the microphyllous forms, but is found equally among the primitive ferns.

In dealing with the problem of symmetry in the sporophyte, the author seeks to show that "the radial type of symmetry is the prior condition for the sporophyte at large" (p. 203). No one could dispute this in relation to the Bryophytic sporogonium, though we cannot concede that any presumption as to the Vascular plants is involved in such an admission. At the same time we must frankly grant that we are impressed with the trend of the facts collected by Professor Bower to support the conclusion that the primitive symmetry of the Pteridophytic sporophyte is also radial, even in the Ferns. Such a conclusion, while in no way militating against the origin of the Vascular plant from a branching thallus, is certainly *pro tanto* opposed to the theory of its origin from a dorsiventrally organised thallus.

In discussing the interesting question of "The establishment of a free-living Sporophyte" (Chap. XVII.) the author assumes, in accordance with his general theory, that the sporophyte being evolved from a sporogonium was originally completely dependent

on the gametophyte. He dismisses in a slightly contemptuous paragraph at the end of the chapter the view that it might have been free-living throughout its life, as it is in *Dictyota*. It is only necessary here to remark that such a hypothesis is not *prima facie* ridiculous, but at the same time it is no necessary complement of the view that the sporophyte was originally a thallus and not a sporogonium. Professor Bower does not definitely commit himself to any theory of the phylogenetic origin of the root. He merely states the alternatives that it may have "resulted from the transformation of a leafy shoot by loss of the appendages, followed by other special adaptations in relation to its life, and to its absorptive function in the soil"; or that "it arose as a new type of haustorial outgrowth, not originally of shoot-nature." He is inclined to accept the latter alternative. The phylogenetic position of the "protocorm" is then considered and the conclusion reached on good grounds that it probably does not represent an ancestral phase of embryonic structure even for the genus *Lycopodium* as a whole. With the author's general conclusion that the origin of the root-system of the sporophyte is "quite as obscure as that of the leafy shoot itself" we agree, but would suggest that the difficulty is made less by supposing the root to represent a thallus-branch which shared the characters of the aerial branches of the primitive sporophyte and has retained such of them as are adapted to its life conditions and functions. The "rhizophores," and similar structures whose morphological nature has always been a difficult problem, would then appear as modifications of the primitive type of branch, and the difficulty we feel of understanding why a "haustorium" should "resemble the shoot from which it arose in its structure and in the character of its branching" would be removed. This kind of difficulty is inherent in the attempt to derive a plant from a sporogonium, and can only be met by more or less gratuitous hypotheses.

In discussing "the evidence from Palæophytology" the author calls attention to the fact that the fossil record is silent on all questions relating to the "prime origins" of the leafy sporophyte, this being no doubt largely due to the fact that this origin must have taken place long before the earliest rocks from which fossils are recorded were laid down. There are nevertheless certain palæontological facts, already alluded to, which, so far as they go, certainly do not tend to support the "strobiloid theory." There is the early existence of relatively megaphyllous plants belonging to or allied with the Equisetales, and there is the entire absence of any fossils suggesting relative microphyllly among the earliest known Ferns.

In analysing the factors causing "amplification and reduction" in the course of evolution, Professor Bower shows reason to believe that the latter process has been over-rated in the discussion of the relationships of more or less isolated forms, and very rightly points out that good grounds should be assigned for invoking a general process of reduction in any given case. The mycorrhizal Pteridophytes he thinks show little evidence of a general replacement of autotrophy by heterotrophy such as would involve any considerable reduction of the chlorophyllous system. In certain cases he sees an increasing dependence of the sporophyte (or sporogonium) upon the gametophyte, leading to an effective reduction of the assimilatory apparatus of the former.

The concluding chapter of the First Part of the book is a useful "summary of the working hypothesis," which contains, of course, nothing that has not been dealt with in the earlier chapters.

Part II. is occupied with a detailed statement of the facts of the morphology and development of the sporophyte throughout the Archegoniate series. It is really a treatise on this subject, coloured to some extent by the author's strobiloid theory of the origin of the sporophyte. It is out of the question in the present review to attempt to follow the author through this part of his work, nor is it necessary to do so in order to obtain a just idea of his theoretical position and the evidence on which it is based. As the reader will have gathered from what has been written, the "Statement of the working hypothesis" is so full, and so many facts are cited and discussed, that the "detailed statement" scarcely lends material additional support to the fabric already erected.

On the other hand of course Part II. provides the student with a rich storehouse of facts skilfully set out by a real master of the subject. Our knowledge of this branch of botany has increased so rapidly of late years and the author has played so large a part in building it up, while at the same time he commands such a clear and easy style of exposition, that this treatise will necessarily at once take its place as by far the best available. If we may single out individual chapters which appear specially excellent, they would be those on the Ophioglossales—quite a masterly analysis of the facts known about this isolated group (though we think there is a good deal more to be said than the author would lead us to suppose in support of the view that *Ophioglossum* is reduced rather than relatively primitive), and the later chapters on the Ferns, containing the author's most brilliant and convincing work on the sorus and sporangium of the Leptosporangiatæ.

With regard to the work as a whole, we are inclined to believe that the author would have done better to have made two books on the subject, one a comparatively short work setting forth his theory of antithetic alternation supported by all available relevant facts, a frankly controversial work, but including a very careful and detailed examination of the objections to his views; the other a comparative morphology of the Pteridophytic sporophyte, detailed and as impartial as might be, with the controversial element reduced to a minimum. It might be replied that this is what he has given us in Parts I. and II. of the present book, and so in the main it is, yet we cannot but think that each would have been better if it had been kept separate from the other, and conceived in a distinct spirit. Nor can the reader quite avoid the feeling that there is an air of the *chose jugée* about the whole discussion so far as it bears on the antithetic theory.

The title is not altogether fortunate as a description of the contents of the work. By far the greater part of the book deals with phenomena which have little or nothing to do with the origin of a land-flora, except in the sense in which all the phenomena of the structure and life histories of vascular plants have to do with it. As a matter of fact there is strikingly little discussion of the actual origin of land-vegetation. And "the facts of alternation" is an incomplete description of what is meant. The phenomenon of

alternation in nature is not confined to the "alternation of generations." A really descriptive title would have been "The morphology of the Archegoniate sporophyte in the light of the theory of the antithetic origin of alternation of generations." This is not nearly so attractive a title as the author's, but there is a good deal to be said for accuracy of description in scientific titles.

But when all criticisms have been made we may acknowledge gladly and gratefully that Professor Bower has laid the botanical world under a great debt by publishing a book so full of skilfully arranged fact and able analysis, a book easily excelling, in thoroughness of treatment and in intimate first-hand acquaintance with the phenomena discussed, not only any existing work, but, it is safe to say, any work on the subject that could have been produced by any other living botanist.

A.G.T.

REVIEW:

RECENTLY PUBLISHED CATALOGUES OF BRITISH PLANTS.

LIST OF BRITISH SEED-PLANTS AND FERNS. London: The British Museum, 1907. [Compiled by Jas. Britten and A. B. Rendle.]

LIST OF BRITISH PLANTS, by G. C. Druce. Oxford: The Clarendon Press, January, 1908.

THE LONDON CATALOGUE OF BRITISH PLANTS. Tenth Edition. London: George Bell & Sons, February, 1908. [Edited by F. J. Hanbury.]

A CENSUS CATALOGUE OF BRITISH MOSSES. York: Coultas and Volans, 1907. [Edited by Wm. Ingham.]

THE almost synchronous appearance of three catalogues of British vascular plants would seem to denote a much greater interest in field botany in this country than most people have been inclined to suspect. Of course, the adoption of International Rules of Botanical Nomenclature by the Botanical Congress at Vienna in 1905, is primarily responsible for the production of the new Museum and Oxford Catalogues, and of the new edition of the well-known London catalogue. There is probably not a sufficient demand for the continued sale of all three catalogues; and the operation of the law of natural selection will, we fear, result in an early elimination of the Museum catalogue. The absence, from this list, of varieties, of hybrids, of aliens, of extinct species, of an index of common British names, of Channel Island species, and, in fact, of all topographical information including even census numbers is fatal to its successful competition with its more virile rivals; added to which a rather serious misprint in the numbering of the genera, and an irritating (but very necessary) list of corrections, published by the authors in a contemporary not in the hands of all purchasers of the catalogue, would seem to indicate a lack of that inherent vitality which is necessary in a successful struggle for existence. The Museum catalogue was the first of the three to be introduced after the adoption of the Vienna rules; and, although the lengthy list of corrections would appear to indicate that the catalogue had been compiled with undue haste, yet its simplicity of arrangement, its low price, its useful synonyms, and its index of orders arranged according to modern views of affinity are all excellent characters which make us regret its inevitable consignment to the category of excluded forms.

The Oxford catalogue is the most ambitious of the three; and herein, perhaps, lies its weakness. The Museum catalogue represents one extreme of simplicity, the Oxford catalogue the other extreme of complexity. Mr. Druce's elaborate citation of synonyms and authorities, his almost interminable array of varieties, hybrids and aliens, will, we feel sure, be regarded as wearisome by the rank and file of field botanists. As an example of the extreme to which Mr. Druce, in a laudable effort to make his list as catholic as possible, goes in the direction of cataloguing aliens, we may mention that the vine, the fig, the orange and the date-palm are honoured by a position in this Oxford list of British plants! Further, whilst we believe that most British botanists will sympathise with Mr. Druce's outburst against the favoured list of "Nomina Conservanda," which was unwisely and hurriedly adopted by the Vienna Congress, we also feel that his definite refusal to follow *in toto* the Vienna rules will be regarded as an example of not playing the game. To have played the game, Mr. Druce should have adopted the whole of the Vienna decisions, advocated certain obviously necessary alterations at Brussels in 1910, and endeavoured to secure the presence at Brussels of a sufficient number of British and American botanists to ensure a majority in the voting. Mr. Druce's additional use of the capital letter for specific names ending in *-oides* is also vexatious; and his reason for the proposed innovation is not, in our judgment, sound. On the other hand, the details of the Oxford catalogue are, in many cases, of great value to critical field botanists, most of whom will doubtless, in spite of its inflated price, possess themselves of a copy. Whether or not the catalogue will be financially successful is a matter which may be left to the Clarendon Press syndicate.

The London catalogue retains its familiar features; and the addition, in certain cases, of useful synonyms considerably augments its value. A further important point in its favour is its grouping of critical species into larger units in the case of *Rubus* and *Hieracium*; and this plan should, in our opinion, be adopted in a large number of other genera. In the matter of cataloguing varieties and aliens, and of citing authorities, it takes up a commendably moderate position. The catalogue is well printed, and has a very neat appearance, in which regard it contrasts most favourably with the product of the Clarendon Press. There are very few misprints and omissions; and its reasonable price will further enable the London catalogue to retain its premier position as the standard list of British vascular plants.

The treatment of colonists and aliens in the London catalogue is inconsistent. For example, all the *Papavera* are marked by an asterisk to indicate that they are not truly indigenous; whilst all the *Fumaricæ*, most of the *Brassicæ*, and many other weeds are treated as natives. *Papaver somniferum* is not degraded to the rank of a casual or planted alien, whilst *Impatiens parviflora* and *Claytonia sibirica*, both of which have been established for many years in certain woods in the north of England are so degraded. On the whole, however, this portion of the London catalogue has been by no means badly done; and its refusal to ear-mark denizens, or species more or less doubtfully native, is praiseworthy, though it must be borne in mind that the catalogue does not pretend to settle disputes relating to the citizenship of species.

Minuartia verna Hiern is given as the name of the lead-wort in the Museum catalogue; whilst the still later Oxford and London catalogues give the plant under the name *Arenaria verna* Linn. The Cheddar pink, in the Museum catalogue, is given under the name of *Dianthus gratiopolitanus* Villars; but from the authors' subsequent corrections, we gather that they relinquish this name in favour of *D. glaucus* Huds. The Oxford catalogue, however, gives the ugly name of Villars, and simply quotes as synonyms the names *D. caesiuss* Sm. and *D. glaucus* Huds. From this confusion, we are, for the moment, at least, recovered by the London catalogue, which adopts the name of Hudson. A perusal of the notes and corrections by Messrs. Rendle & Britten should convince botanists that, in spite of the Vienna Congress, we are still some considerable distance from finality in the matter of the names of plants; and as such insoluble questions arise as what constitutes publication and what constitutes description, it would appear that nothing short of the adoption of a list of standard names by some future Congress will ever bring, in certain disputed cases, the desired finality.

Taking the London catalogue as the last word (up-to-date) on the subject, we note that the genus *Ranunculus* is substantially unchanged, the "splitters" apparently having done their worst with the crowfoots some years ago; and the genera *Thalictrum*, *Fumaria*, *Cochlearia*, *Brassica*, *Epilobium*, *Salix*, *Potamogeton*, and some others, are also saved from much further sub-division by the systematists. Their energies, however, have not lain dormant, for the genus *Salicornia*, which formerly had two species, now has eight; and the genus *Euphrasia*, which formerly had one species, now has fifteen, exclusive of twelve hybrids, a variety, and a *forma*. The genera *Rubus* and *Hieracium* are still running their neck-and-neck race for numerical supremacy: both are going strongly, and, at the present moment, the odds are slightly in favour of the hawkweeds; nor is there any certain indication that the end of the race is in sight.

The following changes (*inter alia*) of generic names have been adopted: *Radicula* vice *Nasturtium*, *Nymphoides* vice *Limnanthemum*, *Limonium* (pro parte) vice *Statice*, *Centaureum* vice *Erythræa*, *Helleborine* vice *Epipactis*, and *Phyllitis* vice *Scolopendrium*. After all these years of *Calluna Erica*, we revert to *C. vulgaris*; and (*inter alia*) *Molinia cærulea*, *Mænchia erecta*, *Rosa spinosissima*, and *Primula vulgaris* furnish further illustrations of synonymic atavism. *Erophila vulgaris*, our old friend "*Draba verna*" (a synonym which exhibits only a trivial sign of reversion) becomes *E. verna*. "*Potentilla Tormentilla*," after several years of *P. sylvestris*, now appears as *P. erecta*. *Ulex nanus* becomes *U. minor*, and *Potentilla Fragariastrum* becomes *P. sterilis*. *Conopodium denudatum* (= "*Bunium flexuosum*") is now *C. majus*. *Stachys Betonica* yields to *S. officinalis*, *Parietaria officinalis* to *P. ramiflora*, and *Alnus glutinosa* to *A. rotundifolia*. "*Scilla nutans*," Protean in its appellations, is henceforth to be spoken of as *S. nou-scripta*.

Populus canescens disappears as a species, and is catalogued as a hybrid. *Hieracium* is now destitute of a single hybrid, but has over 150 varieties and *formæ*, in addition to more than 130 "species." On the other hand, *Epilobium*, with only 13 species, has 33 hybrids, but not a single variety. We wonder if the evidence on which these hybrids are founded is invariably sound.

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Cratægus Oxyacantha has become two separate species, the old name being retained for the less common form; and the commoner form, formerly considered as a variety, becomes *C. monogyna*. *Taraxacum Dens-leonis* has become four species. For ourselves, we think the sub-division of legitimately divisible species may serve a useful purpose. Some of the segregates are possibly the "ecads" of Professor Clements: others are probably the "elementary species" of De Vries; and generally most of them are worth serious study from the modern points of view. But we should like to see an arrangement of species which would indicate the closely allied segregates and the remotely allied aggregates (on the lines possibly of Hooker's *Students' Flora*) when the working out of the significance of these multiple forms could, at least, be presented to posterity as a problem capable of solution. At present, the catalogue does not present any harmonious notions as to the value of genera, species, varieties, and forms; though we freely admit that each succeeding edition of the catalogue is, in this respect and along what we may perhaps term Jordan's lines, an advance on its predecessor. The catalogue, however, aims at utility; and, until some such method of indicating the allied segregates is found, the utility of the catalogue will remain seriously at fault. We put forward this point of view in all seriousness to the critical systematists whose labour of love it is to revise the more difficult genera.

We are also strongly of opinion that the time is now ripe for the consideration of the question whether or not the arrangement of orders according to the *Genera Plantarum* of Bentham and Hooker should be superseded by that of the *Pflanzenfamilien* of Engler. There are certain details of the arrangement of Bentham and Hooker, which, we are pleased to note, the Oxford catalogue modifies; but the retention, by both the London and Museum catalogues, of the Gymnosperms, in their old place between Dicotyledons and Monocotyledons is a serious anomaly in the light of established knowledge. The least that the eleventh edition of the London catalogue should do is to place the Gymnosperms between the Angiosperms and the Pteridophytes, and to give an alternate list of cohorts and orders arranged according to modern views of affinity. An eleventh edition of the catalogue will become a desideratum after the results of the Brussels Congress in 1910; and we hope the Editor and his collaborators will consider the possibility of adopting the friendly suggestions we have here made.

The catalogue of mosses is a straightforward attempt to provide a standard list of British mosses, arranged according to the latest views. The mosses are named in accordance with *The Students' Handbook of British Mosses* (Dixon and Jameson), except the *Sphagna*, which are arranged according to Warnstorff's system. The distribution of the species and varieties is indicated by means of numbers—those of H. C. Watson's 112 divisions of Great Britain and R. Lloyd Praeger's 40 divisions of Ireland being used. This is an excellent plan, which we wish it were possible to adopt in the case of the London catalogue. There can be no doubt that both this and the London catalogue ought to be in the hands of all botanists interested in field work.

C. E. Moss.

THE

NEW PHYTOLOGIST.

VOL. VII., Nos. 6 & 7.

JULY 31ST, 1908.

OBSERVATIONS ON THE OSMOTIC PROPERTIES OF
THE ROOT HAIRS OF CERTAIN
SALT MARSH PLANTS.

BY T. G. HILL.

[WITH FOUR TABLES AND TEXT FIGS. 21—24.]

THE factors, historical and physical, influencing the life-histories of plants, considered both as individuals and as members of communities, are of some considerable complication, and our knowledge of them could hardly be described as profound. The condition which determines the presence or absence of any particular plant in any particular locality is the resultant of these factors, which must be separately investigated before the resultant can be determined; and this, presumably, is the ultimate aim of field-physiology, or, to use the more current term, *œcology*.

The work carried out on the salt-marsh known as the Bouche d'Erquy, in Brittany, by Professor F. W. Oliver and his comrades, of which the present communication is an outcome, has this end in view.

The most characteristic feature of the low-lying region mentioned, is the periodical inundation by the tides, the result of which is that the soil is saline to a greater or lesser extent according to various physical features. Further, the degree of salinity in any one spot is not a constant, for it obviously depends on the high tides, which are often sufficiently high to flood the whole of the area, and, at the other extreme, so low as to cover none of the parts under vegetation. Thus a region which is covered only by the highest tides becomes, during the intertidal cycle, more and more saline, especially during periods of relative drought, and, of course, all localities after rain are less saline.

It was considered desirable to have some information regarding the effect of rain on the salinity of the soil; Nature afforded an opportunity by sending a never-to-be-forgotten downpour on the

night and morning of September 10th and 11th, 1905. The two following tables set forth the results obtained from three different stations¹.

Table 1 shows the amount of rainfall on the specified days, and the salinity of the soil-water—estimated as chlorides—taken from definite stations; the second table is an attempt to illustrate the results expressed by figures in the first table, together with the high tides. It may be remarked that in the second table, the lines connecting the various salinities of the soil-water from the different stations do not represent the actual curves of increase or decrease in these salinities; they are used merely to connect the points referring to the same station, in order to facilitate reading.

It is necessary to add that station 1 is situated on a low plateau which is covered by a community of *Glyceria maritima*, *Suaeda maritima* and *Salicornia herbacea*. The level of this spot is sufficiently high to be untouched by tides less than about 37 feet. Station 6 is a pan, devoid of vegetation, the earth of which is argillaceous in character and is covered by tides over 39 feet. Station 18 is a patch of bare sand which is inundated by tides higher than 33 feet. Finally, the salinity of sea-water at Erquy is about 3.15%.

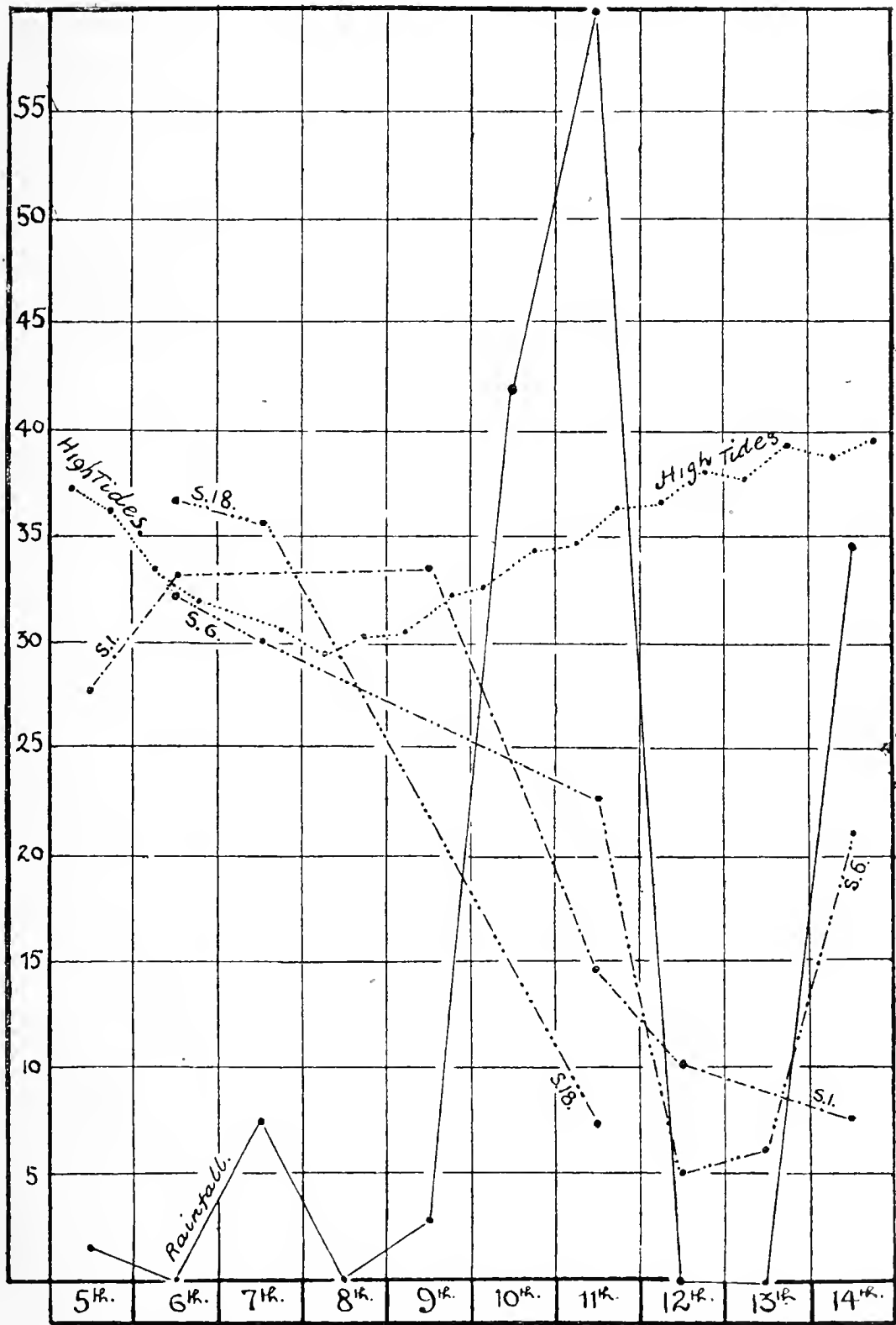
TABLE I.

Date.		Rainfall.	Salinity of Soil Water.		
Sept., 1905.			Station 1.	Station 6.	Station 18.
5th	...	·015"	2·77%	—	—
6th	...	·0"	3·31%	3·21%	3·67%
7th	...	·075"	—	3·02%	3·58%
8th	...	·0"	—	—	—
9th	...	·03"	3·35%	—	—
10th	...	·42"	—	—	—
11th	...	·60"	1·47%	2·28%	·74%
12th	...	·0"	1·01%	·52%	—
13th	...	·0"	—	·62%	—
14th	...	·347"	·79%	2·12%	—

It is seen that in all cases the effect of the rain was to wash out the salt from the soil, although the time taken varied at the different stations owing no doubt to the percolability and other physical characters of the soil.

¹ These analyses were made by the "chemical section" of the field party working under the direction of Dr. F. F. Blackman.

TABLE II.



Rainfall (in hundredths), _____ Tides (in feet),
Salinity of Soil-water (per thousand); of Station
1 - - - - -, of Station 6 - - - - -, of Station 18 - - - - -

This being so, various questions arise. What is the effect of such differences in the salinity of the soil upon the plants? How does the plant accommodate itself to the fluctuating concentration of the soil-water? What is the osmotic condition of the cells of the plants?

Hitherto, the chief work on osmosis at Erquy had been carried out on the cell-sap of the aerial parts of the characteristic plants (*Salicornia* and *Suaeda*), and, although the results obtained were of interest, they do not afford much information in this particular connexion, *viz.*, the osmotic properties of the plants in connexion with the variability in the salinity of the soil-water, inasmuch as these members are not organs of absorption. For this reason attention has been paid to the osmotic properties of the root-hairs, which work has been done in the spring-time on seedlings owing to the practical impossibility of successfully washing out the soil from the roots of mature plants without damaging the regions of the active root-hairs.

The investigation was commenced in April, 1907, and the first feature to be investigated was the osmotic equivalent of the cell-sap of the root-hairs.

The following table represents the results;—

TABLE III.

Locality.	Plant.	Osmotic Equivalent.
Tansley's Pan. ¹ <i>Salicornia</i> 6·7% NaCl
" ...	" ...	6·73% " *
" ...	<i>Suaeda</i> ...	6·7% " *
" ...	" ...	6·73% " *
Station 1 <i>Salicornia</i> 5·8% " *
" 4 ...	" ...	6·26% " *
" 4 <i>Suaeda</i> 6·26% " *
Ploughed field ...	Mesophyte Seedling ²	... 1·5% " *

These observations were of a preliminary nature: on allowing the seedlings to remain bathed in the solutions of sodium chloride in serial decreasing concentrations, it was found to be a matter of considerable difficulty to determine exactly the osmotic equivalent of the root-hairs; it always appeared slightly lower than the saline

¹ A pear-shaped pan south west of Control-Stations 8 and 9.

² In all probability a Composite.

Results marked thus were obtained by Professor F. W. Oliver independently of the writer.

solution in immediate use. As this occurred frequently, fresh seedlings of *Salicornia* were removed from the earth and examined in a molecular solution of common salt; if the root-hairs resisted this concentration, and showed no plasmolysis, the plants were placed in fresh, or very slightly saline water, for varying periods of time, at the conclusion of which the osmotic equivalent of the root-hairs was determined.

TABLE IV.

Locality.	Period of Soaking.	Osmotic Equivalent.
S—4 5 hours ..	2·4% NaCl
S—4 12 „ ...	1·91% „
Tansley's Pan 18 „ ...	3·31% „

These results (Table IV.) indicate that the osmotic strength of the cell-sap of the root-hairs varies with the concentration of the surrounding medium, being lower when the external solution is weaker and, on the other hand, is greater when the concentration of the surrounding solution is higher: a result which is in agreement with those obtained by Mayenburg¹ and others for fungus hyphæ. This being so, it appeared unnecessary to determine the *exact* osmotic equivalent, and in the following experiments this was not done in all cases. The root-hairs of fresh *Salicornia* seedlings were tested to see whether they could resist a 5·8% solution of common salt; all so proved could, and they were then soaked in a 1% solution of sodium chloride for two hours, after which treatment they were found to be plasmolysed in the original 5·8% solution of salt.

Similar experiments were performed by allowing the sod, containing the seedlings *in situ*, to soak for eighteen hours in stream-water, and testing a few seedlings from it before and after the soaking. Previous to immersion in the fresh water, the root-hairs resisted the molecular solution of salt, but after the washing-out they were readily and much plasmolysed by a solution of the same strength; subsequently, the internal osmotic pressure was found to be equivalent to a 3·31% solution of chloride of sodium.

These results, obtained in the spring of 1907, clearly show that the root-hairs of *Salicornia*, growing in places where the soil-water is strongly saline, can accommodate their internal osmotic pressure as the salinity of the water of the surrounding medium falls in concentration.

¹ Prings. Jahrb. f. Wiss. Bot., 36, 1901.

It remains to be demonstrated whether they are capable of *raising* their internal osmotic strength in proportion to the increase of the external salinity, which part of the investigation was carried on during April of this year.

In order to show this, sods containing seedlings of *Salicornia* were taken from a pan which had been covered by the tide a few hours previously. The turf was placed in a dish of fresh water, which was changed periodically, so that the salinity was gradually reduced. From time to time a seedling was removed and its root-hairs tested with a 3.5% solution of sodium chloride. Eventually nine consecutive seedlings showed a marked plasmolysis of their root-hairs. These were allowed to remain in a bath of saline of the stated strength (3.5%) and were examined next morning; when it was found that, of those root-hairs which were favourable for observation, 81% showed no plasmolysis, and the remaining 19%, although slightly plasmolysed, were not affected to anything like the same degree as when they were first examined. At the first immersion in the 3.5% solution of sodium chloride, the protoplasm shrank away, not only from the top of the root-hair, but also from the sides (Fig. 21); at the second test, the appearance of the plasmolysis, in the cases where it occurred, was as illustrated in Fig. 22.

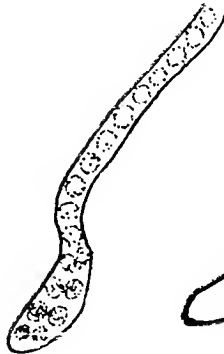


Fig. 21.

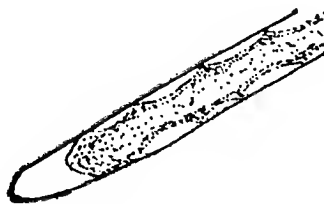


Fig. 22.

In order that the natural conditions might be reproduced as nearly as possible, a portion of the soaked sod was bathed in a 3.5% solution of salt, which was sufficiently strong to plasmolyse the sample seedlings examined. After the treatment, the result was found entirely to confirm the results of the preceding experiment.

The following observations were then made on the hairs of a restricted area of the roots of a fresh batch of *Salicornia*, which had been previously treated with fresh water. Of these, rough charts were drawn in order that the same root-hairs could be kept

under observation; all of which, in a preliminary trial, were strongly plasmolysed by a 3.5% solution of sodium chloride. The seedlings were then rinsed in dilute saline, and were brought up through successive concentrations to a 3.5% solution; after being allowed to remain in this for some time the root-hairs were again examined. Of the five seedlings taken, the root-hairs of four showed a practically complete recovery, being now not plasmolysed by the 3.5% solution of salt, which, previously, affected them strongly. The fifth seedling, however, showed many hairs which had not recovered their turgidity; the treatment was therefore continued, but the result was the same. The anomalous behaviour of this seedling being inconsistent with the experience gained from the previous experiments, it was considered possible that the earlier treatment had been too severe, and that the seedling, or at any rate the root-hairs, were in an unhealthy condition. In order to see whether this was the case, the plant was placed for definite periods of time in successively weaker solutions of salt, *viz.* 3%, 2.4%, 1.7% and lastly fresh water. After each successive bath, the root-hairs were still found to retain their plasmolysed condition, and this, even after a prolonged treatment with fresh water. It was thus clear that the hairs were either dead, or were in a condition of so low a vitality as to preclude their recovery. Consequently the results given by this particular seedling may be rejected; in no way do they invalidate those afforded by the other individuals.

The observations here recorded show that the root-hairs can accommodate their internal osmotic pressure in proportion to the osmotic strength of the soil-water. This, of course, is what we should expect from theoretical considerations, but, at the same time, the experimental results may be of interest and not without value in providing concrete examples of the adaptability of root-hairs, and in confirming conclusions based on theory.

Attention may here be drawn to the interesting work of Osterhout,¹ who showed that marine Algæ attached to the sides of steam-boats may be subjected to great ranges in the salinity of water, the daily change being from saturated sea-water on the one hand, to perfectly fresh water on the other. He further² suggests that osmotic pressure may play but a small part in the

¹ Osterhout. The resistance of certain Marine Algæ to changes in osmotic pressure and temperature. Univ. Calif. Publications, Vol. II., No. 8, 1906.

² The rôle of Osmotic Pressure in Marine Plants, *Id.*, No. 9, 1906.

vital processes of plants which are generally supposed to be very sensitive to changes in the osmotic pressure of the surrounding medium. A conclusion based on the following observations:—

1. Delicate marine Algæ taken from the sea and placed in fresh water grew for months.

2. Plants transferred from ordinary sea-water directly to saturated sea-water, flourished for one or two months.

3. Algæ taken from the sea lived for relatively long periods in sea-water to which had been added three or four volumes of distilled water.

It is clear that these observations are of the same nature as those considered in the present communication; and it does not appear unreasonable to presume that the marine Algæ have the same power of rapidly adjusting their internal osmotic strength, according to the salinity of their surroundings, in the same way as salt-marsh plants. In other words, osmosis is a far more delicate mechanism, in the living organism, than Osterhout's conclusion would lead us to suppose, and this is probably the explanation of the above facts observed by Osterhout.

Drabble and Lake¹ also have published valuable results which bear upon the present observations. They have found that "a greater concentration of cell-sap occurred in those plants which had been most strongly subjected to factors tending to promote loss of water by transpiration." Thus *Taraxicum Dens-leonis* growing in damp long grass near a water-course showed a low osmotic equivalent, while *Vaccinium myrtillus* growing on rocks was shown to have a comparatively high osmotic strength. Further, *Geranium Robertianum*, growing near a salt marsh, had a slightly lower internal osmotic strength as compared with another individual of the same species, growing on rocks at some altitude. In a later publication² these same authors have shown that:—

1. The osmotic strength is least in submerged fresh-water plants and greatest in salt-marsh plants.

2. The greater the physiological drought under which the plants are accustomed to grow, the greater the osmotic strength of the sap of the turgid cell.

¹ Drabble and Lake. The osmotic strength of cell-sap in plants growing under different conditions. NEW PHYTOLOGICAL JOURNAL, IV., 1905.

² The relation between the osmotic strength of cell-sap in plants and their physical environment. Bio-Chem. Journal 11., 1907.

3. In any area the osmotic strength varies with the physiological scarcity of water.

4. In all plants growing under the same conditions the osmotic strength of the cell is generally the same.

In all cases the authors used either the epidermis or the mesophyll of the leaf.

The results obtained from the study of *Salicornia* and *Suaeda* are in agreement with those of Dr. and Mrs. Drabble, with possibly two exceptions. Firstly, my observations tend to show that there is a variation in the osmotic strength of different individuals growing in the same locality; and, secondly, the osmotic equivalent of salt-marsh plants may be very much higher, in fact, double that given (.51 gm. mol. of NaCl.) by our authors. These divergencies are probably of no importance; for, in the first case, the seeming difference may be due to the fact that leaf-tissue was used in the one investigation and root-hairs in the other. In the second instance, the plants used were not the same; also, it has been shown how great may be the variation in the osmotic strength of one cell at different times, when subjected to different conditions; and, lastly, our authors do not give any observations on the salinity of the soil-water, which is an important factor bearing on the osmotic strength of the plant, and which might have been less at Burton Point, Cheshire, than that which obtains at the Bouche d'Erquy.

To return to the salt-marsh plants; it is not proposed to discuss, on the present occasion, the mechanism by means of which the internal osmotic pressure of the root-hairs is regulated: it may be due to chemical changes in the organic substances of the cell-sap, or, to the absorption of sodium chloride from the surrounding medium. As regards this last possibility, it may be remarked that no trace of sodium chloride was found in the root-hairs on a preliminary analysis; but this is a point which will have to be more fully investigated.

The following is a summary of the chief facts observed, other than those dealt with above.

1. The osmotic pressure in different root-hairs of the same individual plant varies; as a rule the younger hairs have a higher equivalent. The cells of the root-cap have a very low coefficient.

2. The osmotic pressure in the root-hairs may vary in different individuals of the same species.

3. On transferring isolated seedlings from relatively strong saline solution to fresh water, the tips of the root-hairs may swell out and assume curious shapes (Fig. 23).

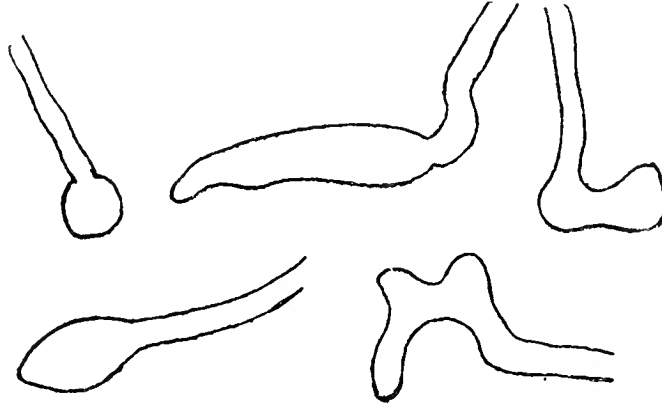


Fig. 23.

4. Occasionally, branched root-hairs may be seen (Fig. 24).

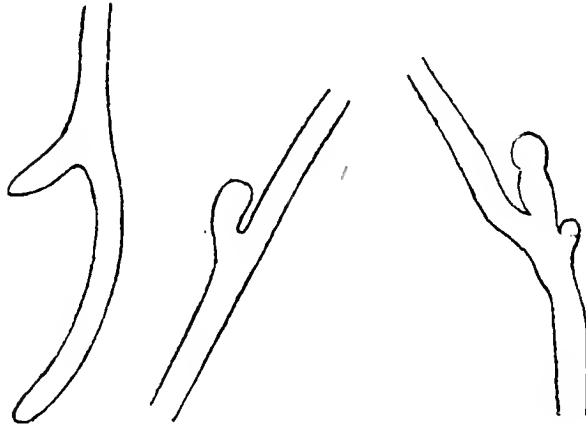


Fig. 24.

5. The cellulose-wall of the tip of the root-hair may be thickened (Fig. 22), which may possibly be of value in giving the end a greater strength in order that a sudden increase in the internal pressure, due to a sudden diminution in the osmotic pressure of the soil-water, may be withstood.

6. The amount of sodium chloride in the seedling seemingly increases from the root upwards. The salt is most abundant in the higher region of the hypocotyl, and in the fleshy cotyledons.

THE SPORANGIOPHORE—A UNIT OF STRUCTURE IN
THE PTERIDOPHYTA.

By M. BENSON, D.Sc.

[TEXT-FIGS. 25, 26.]

ONE of the many contributions to our knowledge of the phylogeny of the Vegetable Kingdom that are due to Palæobotany is the conception of the structure known as a sporangiophore.

As far back as 1900 Dr. Scott brought together in the first edition of his "Studies in Fossil Botany" a series of facts pointing to the wide occurrence of such a body and the great range of form which it might assume.

The number of types known to us has now greatly increased. The range of form in the Sphenophyllales may be from a tetrasporangic to a monosporangic condition; from a sessile to a pedicellate; it may be inserted on a bract or on an elongating axis.

In the Equisetales it may be tetrasporangic or polysporangic. It is generally radially symmetrical, but in the forms known as *Stachannularia* and *Cingularia* it is dorsiventral. It may appear associated with sterile bracts or without them, but is always inserted directly upon the elongating axis.

In the Psilotales the sporangiophore may be bi-sporangic or tri-sporangic. In this recent group variations have also been recorded by Professor Thomas¹ and Miss Sykes², which further accentuate the plasticity of the sporangiophore. Miss Sykes records cases in both *Tmesipteris* and *Psilotum* in which the sporangiophore is terminal on an axis, and in which the structure is monosporangic.

The three sub-phyla thus far referred to are sometimes grouped together under the name "Sporangiophoric Pteridophyta," as, for instance, by Professor Bower in Chapter XXIX. of his "Origin of a Land Flora." In the succeeding chapter, however, he uses the term "sporangiophore" for the fertile part of the leaf of the Ophioglossaceæ. I will discuss the application of the term in this sense in a later paragraph. Yet a second problem arises in connection with the use of this term. It has been again and again suggested that we have in the Lycopodineous "sporangium" a reduced structure which is homologous with the sporangiophore of the

¹ Thomas. Proc. R. S., Vol. LXIX.

² Sykes. Annals of Botany, 1908, January and July.

Sphenophyllales. The evidence in favour of this "reduction hypothesis" is still very inadequate, although Miss Sykes's work on the "Sporangium-bearing Organs of *Lycopodium*¹" has shown the wide range of form and structure that the "sporangium" exhibits.

For the sake of comparison with her results it may be interesting to refer to two Palæozoic types of Lycopodinean "sporangium" which unfortunately still await description. I append diagrammatic figures.

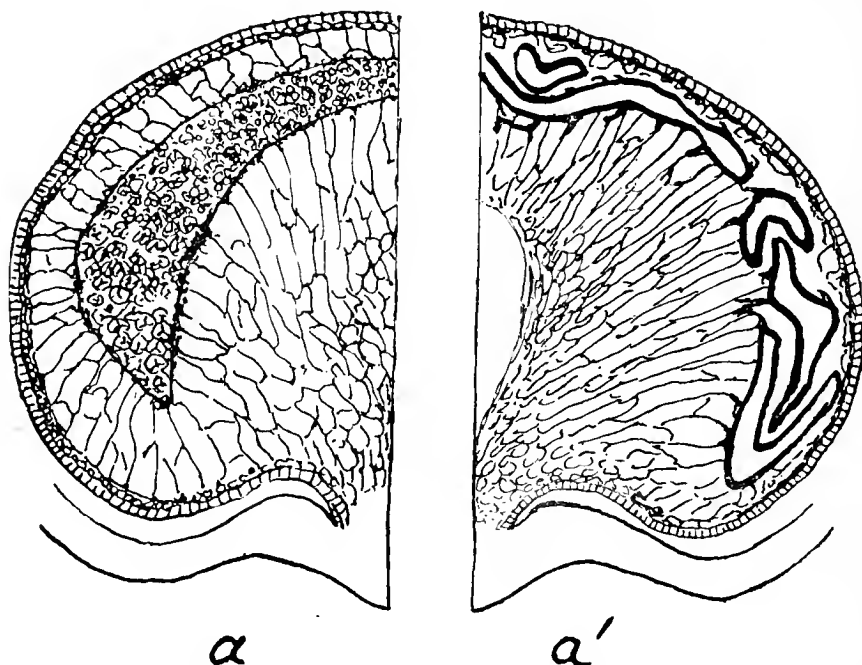


Fig. 25. Diagrams of halves of tangential sections of a micro- and megasporophyll respectively. $\times 30$. Royal Holloway College Collection, C.N., 266.4 and 192n. Both specimens are referred to as *Lepidostrobus Mazocarpon*.

Fig. 25 is from two specimens met with in the Burntisland rock. *a* and *a'* represent halves of tangential sections of a micro- and a megasporophyll of what I assume to be a species of *Lepidostrobus*. They are associated with the branching stems of *Lepidodendron Pettycurensis*, which has recently been shortly described by Mr. Kidston² as showing a solid protostele. Owing to the resemblance in some respects which these sporophylls show to *Mazocarpon* I will refer to them here as *Lepidostrobus Mazocarpon*. They are interesting not only because of the large amount of sterile tissue, but because of its character. A wide layer abutting on the sporogenous regions consists of elongated tapetal cells. The divergence of these cells leads to a split which may be seen in the median plane of the megasporophyll. This is somewhat suggestive of a multiple origin of the sporogenous region.

¹ Sykes, NEW PHYT., 1908, Vol. VII., p. 41.

² Kidston, Proc. R. S. Edin., Vol. XXVII.

If these two figures be compared with Fig. 26, which is a diagrammatic representation of a tangential section of *Mazocarpon*¹ from the Upper Carboniferous Rocks, one sees again a relatively enormous development of sterile tissue which has given rise to the name proposed for this form ($\mu\alpha\zeta\eta$ =a loaf). This extends into ridges on the sporange wall which have been compared with an incipient indusium, but which may be a vestigial structure. The tetrads are here ranged along the two sides, and the space around them was filled with tapetal cells which have perished. One seems

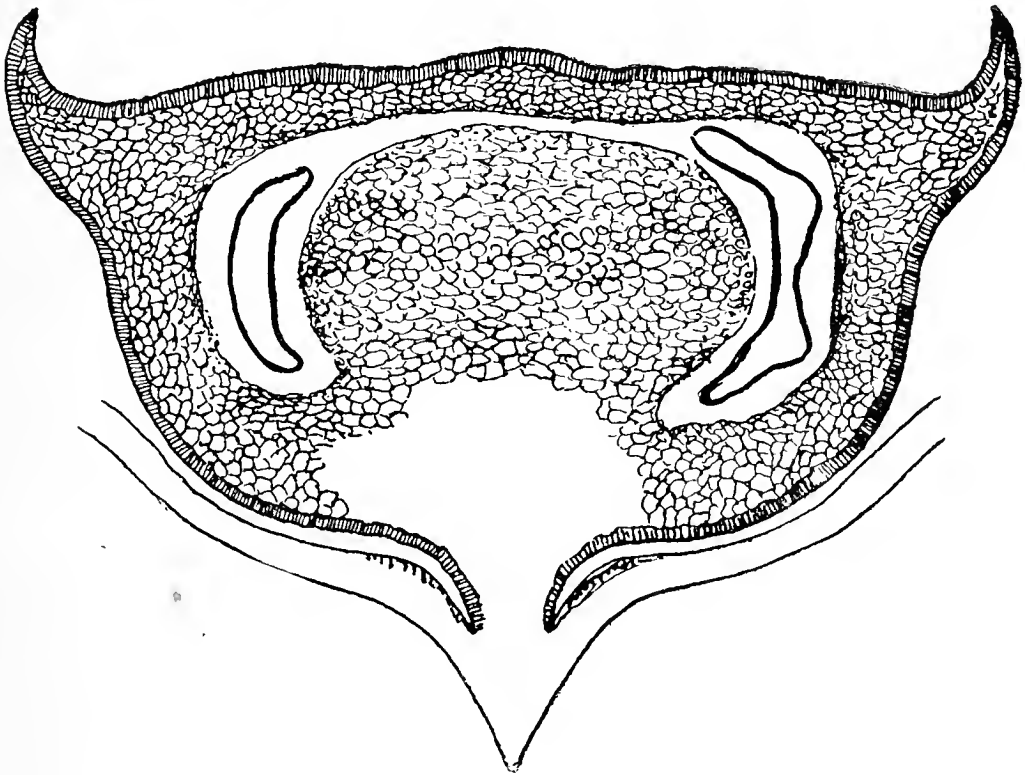


Fig. 26. Diagram from tangential section of a megasporophyll of *Mazocarpon*. $\times 30$. Royal Holloway College Collection of Dalesgate Plants, C.N. 30.

to see in this sporange an explanation of the saddle form of many of the "sporangia" of recent Lycopods, accompanied as such a form is by a well developed "archesporial pad," e.g., in *Lycopodium clavatum*. It would be a very natural sequence that the sporogenous regions of a single sporangiophore should become confluent, and the gradual reduction of the sterile tissue to a mere "archesporial pad" and pedicel would next follow. The inclusion of the Lycopodiales among the "Sporangiophoric Pteridophyta" would make this term as extensive in application as Jeffrey's term Lycopsidea.

But have we even then really reached the full extent of the legitimate application of the expression? Have we no representative

¹ Scott. "Studies," second edition, 1908.

of the sporangiophore in Pteropsida? Is it possible that a body so characteristic of one half of the Pteridophyta should not have its homologue in the other? I wish to lay stress on the resemblances between the synangium or sorus of the Pteropsida and the sporangiophore or synangium of the Lycopsida.

In the vast majority of both Fossil and Recent Ferns the sporangia are aggregated together in tufts or groups, or even in more compact bodies called synangia. Examples of such aggregations are found in the Palæozoic ferns *Diplolabis*, *Botryopteris*, *Zygopteris*, where the constituent members have relatively little cohesion, and in the Marattiaceæ where the cohesion may be complete.

The range in the form and number of parts of the Fern sporangiophore is greater than in that of the Lycopsida, this being probably partly due to the prevalence of the strobiloid habit in the latter.

In the Fern the sporangiophore (sorus) occurs on the margin or lower surface of the frond. In the latter case a peltate form would be a disadvantage, and we see a great contrast in the method of dehiscence of the sorus of *Kaulfussia* and that of *Equisetum*. When the pedicel is continued into a peltate shield as in *Matonia* we find it is caducous. The sporangiophores of Ferns are more comparable in structure with those of non-strobiloid types, such as *Psilotum*. The exceptional cases among the Ferns in which there is no aggregation of sporangia at first appear to present considerable difficulty, and I will refer to them in detail.

I will select *Senftenbergia* and *Archæopteris* for discussion as they are both Palæozoic forms and hence *a priori* might be considered primitive. *Senftenbergia* is essentially of the Schizæaceous type and bears single sporangia at the ends of veins on the under surface of dorsiventral pinnae, while *Archæopteris* may bear its sporangia peripherally on a pinna.

We do not know what were the antecedents of these Ferns, but I would suggest that the scattered condition of the sporangia may be due either to the great expansion and dorsiventral development of the sporangiophore, or to the reduction of a number of sporangiophores each respectively to one sporange. Both of these evolutionary processes are known to occur. In *Acrostichum* most morphologists would accept the view that the loss of the soral identity is due to expansion. In *Dipteris bifurcata*¹ the sorus is still

¹ Armour. NEW PHYT., 1907, Vol. VI., p. 238.

intact and the sporangia are simultaneous in origin, but in *Dipteris conjugata* all stages of the disintegrating process can be seen side by side on the same frond.

Again in *Osmunda* we see an early phase of the loss of soral identity in that the sporangia [of a single tuft face in different directions. A later stage is seen in the scattered sporangia of *Todea*.

Such an explanation might conceivably be applicable to Schizæaceæ, but Prantl's view that the sorus has become monosporangic is far more probable. That reduction of this sort takes place is shown in various degrees among the species of *Gleichenia*, and can be traced ontogenetically in the megasporangial sorus of *Azolla*.

In the case of the Ophioglossaceæ the "sporangium" appears on the other hand to represent a reduced sporangiophore comparable with the monosporangic form found in *Psilotum*. It is not uncommon to find sporangia on the so-called sterile segment of *Botrychium lunaria*. I have also a specimen of *B. lanuginosum* showing the same phenomenon.

In a specimen of *B. lunaria* gathered this season in Yorkshire, and sent me by Miss Beard, B.Sc., the sporangia are rather on the abaxial surface of the margin of the pinnæ. Some of them are stalked and curve over on to the upper surface, and thus bear a curious resemblance to the sporangiophores of *Sphenophyllum Dawsoni*. The dehiscence of each sporangium is effected along a stomium resembling that of the Psilotaceæ. In *Ophioglossum* the fertile spike appears to be a condensed structure with the sporangia sunk in an unbranched lobe of the frond. The existence of such forms as *Marsilia* with fairly typical Fern sori and dorsiventral segmentation of the frond seems to justify us in looking upon dorsiventral segmentation of the frond in Ophioglossaceæ as a character of no great taxonomic value, and as affording no justification for the view that the whole fertile lobe is homologous with the sporangiophore of the Sphenophyllales. I would also strongly deprecate the use of this term in a non-morphological or non-committal sense, a use which is sometimes adopted by Professor Bower in his recent work.

Evidence has gradually been accumulating during the last few years of the convergence of the various groups of Pteridophyta in past epochs. *Pseudobornia ursina*, a most interesting Devonian plant of probably Calamitean affinity, seems to be a type in which the microphyllous habit of the Lycopsida had not yet been evolved.

Protocalamites Pettycurensis, of which much new material has recently come to hand, is a Calamite of Lower Carbiniferous age which exhibits a stelar anatomy comparable with that of many Ferns. Such facts as these point to a monophyletic origin of the Pteridophyta. If the Pteridophyta are monophyletic it would appear that their ancestors possessed a generalized type of sporangiophore. Such a structure must have equally given rise to the "synangium" of *Marattia* and the "sorus" of *Matonia*, to the "sporangium" of *Lepidostrobus*, the "sporangophore" of *Equisetum* and the "synangium" of *Tmesipteris*. Hence I would suggest the following definition of a sporangiophore. A sporangiophore is a structure characteristic of the sporophyte of Pteridophyta, and consists of a central, generally pedicillate, mass of sterile tissue with sporogenous regions occupying either one or more sporangia which may be terminal, lateral or basal. Eventually in some Ferns the sporangia may become completely separated from one another, in which case the common pedicel is obsolete.

MORPHOLOGICAL VALUE OF THE SPORANGIOPHORE.

The hypothesis that leaf and stem are but specialized parts of a common dichotomizing Propteridophytic thallus—an hypothesis which was favourably discussed by Mr. Tansley in the first of his valuable series of Lectures on the Evolution of the Filicinean Vascular System¹, is becoming increasingly important as our knowledge of the earlier Pteridophyta increases. We not only find sporangiophores inserted indiscriminately upon axis or upon leaf, but a more exact knowledge of several of the Palæozoic Ferns has revealed the fact of the existence of adventitious sterile structures which may be inserted either on axis or on rachis.² Hence in both sections of Pteridophyta comparable anomalous structures occur. With the new hypothesis in view such organs may be explained as units of the Propteridophytic thallus which still exist as relics of the condition in which the limits of axis and leaf were not fixed.

The sporangiophore in all known Ferns and in many of the Lycopsidea has been obviously taken up on to the leaf, and it is possible that that was universally the ancestral condition. The appearance of the sporangiophore on the axis in Equisetales, &c., would then be due to a secondary change, which resulted from

¹ Tansley, NEW PHYT., 1907, p. 15.

² Scott, "Studies," Second Edition, 1908, p. 313.

the reduction and chorisis of the leaf during the evolution of microphylls. A leaf wholly composed of sporangiophores, as I interpret the case in *Sphenophyllum fertile*, assists one to realize this conception.

It is, of course, yet possible that Palæozoic ferns may be found with sporangiophores inserted directly upon the axis. I refer to this possibility because in the same way it is conceivable that such ancient seed-plants as *Cordaites* may have derived their spore-bearing organs directly from sporangiophores *inserted on lateral axes*. Such a hypothesis is of course unnecessary, as the commonly accepted leaf-reduction hypothesis could meet the case, but I think there is nothing incredible in the suggestion that throughout the Cordaitales and Taxoideæ we are dealing with plants which have never had their sporangiophores taken up upon leaves, and that, in fact, they are constructed in this respect upon the Equisetal plan, where the sporangiophores are merely associated with bracts.

The "stamens" of *Cordaites* and *Taxus* are radially constructed consisting of a pedicel bearing sporangia. We have in *Torreya* evidence of the evolution of the dorsiventral stamen from such a structure¹. If the dorsiventral stamen of *Torreya* is derived from a radially symmetrical sporangiophore it is probable that that of other Coniferæ has a similar origin.

In these groups of Gymnosperms, and in the Pteridosperms and their descendants (where the sporangiophore is obviously taken up upon the leaf) it seems a reasonable corollary to look upon *the evolution of the seed* as a further elaboration of the megasporangiophore. Space does not allow of a discussion of this problem here.

CONCLUSION.

On the whole, a review of the great central phylum, Pteridophyta, as a group of plants derived from a common ancestor whose sporophyte generation bore a special type of asexual spore-producing organ called a Sporangiphore, seems illuminating and possibly useful as tending to concentrate attention on the probable origin of the structure in question.

¹ Coulter and Land. *Torreya taxifolia*, Bot. Gazette, 1905, p. 159.

THE PHYLOGENY AND INTER-RELATIONSHIPS OF
THE PTERIDOPHYTA.

III.—LYCOPODIALES.

LEPIDODENDRACEÆ AND ISOËTACEÆ.

THE Psilotaceæ are now usually placed in a separate phylum, the Psilotales, between the Lycopodiales and Sphenophyllales. The two genera *Psilotum* and *Tmesipteris* are so closely allied that it will be unnecessary to discuss their affinity to one another. As the phylum contains no other order, the affinity of the Psilotaceæ will best be considered later in treating of the inter-relationships of the phyla.

The first order of the Lycopodiales to be considered is that of the fossil Lepidodendraceæ. The anatomy of some of the stems of the order is very primitive, for in their primary condition they sometimes contained a single, solid, exarch stele, which was probably surrounded by phloem, though the latter appears to have been sometimes ill-differentiated and by no means typical (19). But in most species of *Lepidodendron* and in all known species of the allied *Sigillaria* a medulla has already appeared; the very ancient genus *Bothrodendron*, also belonging to this order, appears likewise to have possessed a pith, but so far the internal structure is known in very few examples. There is little reason to doubt the primitiveness of the solid protostele in *Lepidodendron*; it is also clear that the first step in the further evolution of the stele was usually the formation of a pith; this must have been acquired very early, though in some cases secondary growth in thickness preceded the evolution of a pith (9). In the genera *Bothrodendron* and *Lepidodendron* the ring of wood thus formed appears never to have been broken up into separate bundles. Some species of *Sigillaria* retained a continuous ring of xylem, but others show an evolutionary advance, for the continuous ring though persisting for a considerable distance, is, in parts, broken up into contiguous bundles; others again have advanced a step further, for the ring of wood is in them broken up into separate, but approximated, bundles (14). Thus we see that, as regards the primary anatomy of the axis, the Sigillariæ are less primitive than, and probably derived, from forms of stele such as those of the protostelic and siphonostelic species of *Lepidodendron* and *Bothrodendron*. Secondary xylem is known in nearly all species of any considerable

size except *Lepidodendron Harcourtii* (where its occurrence is doubtful) and *Bothrodendron mundum* (14); secondary cortical tissues are present in all known species. The smaller species without secondary xylem may prove to be portions of bigger ones, or they may be really species without secondary wood. In *Lepidodendron fuliginosum*, a species so like *Lepidodendron Harcourtii* that the two were long confused, a small amount of secondary xylem was produced irregularly by an anomalous cambium. Dr. Scott points out that we may regard this species as exhibiting a primitive and rudimentary or a reduced form of secondary growth (14). But it is by no means certain that some forms of *Lepidodendron Harcourtii* itself had not some secondary xylem. Mr. Seward and Mr. Hill have written a paper on a *Lepidodendron* from Dalmeny, which they regard as probably identical with *L. Harcourtii*. They bring forward only fairly good arguments in support of this suggestion (20), but the geological horizons agree well. The Dalmeny stem, which whether or no it be specifically identical with *L. Harcourtii*, is clearly identical with another species, *L. Wunschianum*, has secondary xylem, and though the question must remain open, it is possible that a certain amount of secondary xylem was usually found in *L. Harcourtii*, but that its formation began very late, many examples being overtaken by fossilization before their primary structure had been modified. In any cases it seems not unlikely that the absence or the rudimentary development of secondary wood in *L. Harcourtii* is a primitive character.

As regards the external markings of the stem, characters on which the division of the order into genera is founded, the scars left by the fall of the leaf are practically identical throughout the order, and consist of a mark of the vascular bundle, of the marks of the parichnos (two parenchymatous strands on each side of it), and of the scar of the ligule above the bundle.

In *Bothrodendron* the scars are flush with the surface, but in *Lepidodendron*, *Lepidophloios* and *Sigillaria*, they are raised on cushions on varying forms. Further, there is Mr. Kidston's genus of *Archaeosigillaria*, in which the scar of the leaf resembles that of *Lepidodendron*, except that the presence of a ligule has not as yet been demonstrated, and that there is no parichnos or leaf-cushion (8). It would seem natural to regard the various forms in which the leaves are seated on cushions as having originated independently of one another from smooth-stemmed types such as *Bothrodendron* and *Archaeosigillaria*, both relatively ancient genera

since they are characteristic of the Upper Devonian and Lower Carboniferous rocks. But last year Mr. White described a form, coming from the Devonian of New York, in which the stem bore both the *Lepidodendroid* and the *Sigillarian* types of marking (28). The fact that such an ancient type should combine the characters of *Sigillaria* and *Lepidodendron* suggests that it, or allied forms, were among the direct ancestors of these two genera; but this fact tells strongly against the tempting view that *Lepidodendron* and *Sigillaria* were evolved separately from a type resembling *Bothrodendron*. Unfortunately Mr. White has not yet published a full account of this curious fossil, so that we do not know how closely it agrees with Mr. Kidston's definition of *Archaeosigillaria*.

Another striking peculiarity found within the order is the pitting of the tracheides in the stem of Renault's *Sigillariopsis Decaisnei* (21). This species is the only one of its phylum in which such pitted tracheides are known, though they are common in other phyla of Pteridophytes. Their significance is thus best considered in discussing the inter-relationships of the phyla.

The leaves of *Lepidodendron* and *Sigillaria* are ligulate and linear-lanceolate; those of *Archaeosigillaria* appear to have been deltoid-lanceolate, and no ligule has yet been recognized in them, though its presence may yet be demonstrated. Renault was the first to describe a double leaf-trace in the leaves of his *Sigillariopsis Decaisnei*. This bifascicular character of the leaves, coupled with the occurrence of pitted tracheides in the stem, had thrown doubt on the *Lepidodendraceous* affinity of this species. The pitted tracheides of the stem have not so far been recognized in any other examples, but Dr. Scott described in 1904 two better preserved examples of *Sigillariopsis*, leaving little room to doubt the *Lepidodendraceous* affinity of these leaves (16). Further, Mr. Kidston's and Mr. Newell Arber's recent investigations make it very probable that the leaf of *Sigillaria* normally contained two bundles, and that the numerous recorded instances of *Sigillarian* leaves with a single bundle are due to the fact that the bundle entering the leaf remained single for a varying portion of its course (10). Until Dr. Scott had described his examples of *Sigillariopsis* (or *Sigillaria* as we may now call them) from the Lower Coal Measures, the only example of a bifascicular *Lepidodendraceous* leaf was Renault's Permian *S. Decaisnei*; it was therefore natural to regard this character as a later development having no relation to the phylogeny of the more primitive members of the order. But now that

it seems very likely that the leaf of *Sigillaria* was characterised by two bundles, the question naturally arises whether the single median bundle of the leaf of *Lepidodendron* is primitive or due to reduction. So far we have little evidence on this point, though it is worth noting that the genus *Lepidodendron* is, as a whole, more ancient than *Sigillaria*. But whichever genus is the more primitive their close affinity is indisputable. One cogent reason for assuming a close affinity of the two genera lies in the apparent identity of their subterranean organs, known to botanists as Stigmariaë. They are dichotomous axes bearing monarch dichotomous appendages. The most important difference between the main Stigmarian axes is that in most species the whole of the xylem is centrifugal, while, in a few cases, a small amount of centripetal xylem occurs internally to the centrifugal wood. In a species recently described by Mr. Weiss this centripetal xylem is remarkably well developed (27). On grounds of comparative anatomy it is clear that the centripetal primary xylem is primitive, and that the forms in which the whole of it is replaced by a pith show a phylogenetic advance. It is, however, strange that the underground organs of so ancient an order as the Lepidodendraceæ should commonly have lost all traces of this centripetal xylem; but the Stigmariaë appear to have been more highly differentiated than the stems to which they were attached. This is evinced by Professor Weiss' demonstration that there are, in the various types of appendage borne by the Stigmarian axes, groups of spiral tracheides in the cortex connected with the protoxylem by narrow bands of spiral tracheides (26). Professor Weiss has shown that this is a secondary modification of the mid-cortical region, tending to improve conduction, but it serves to show the high degree of differentiation which the Stigmariaë had reached, and therefore to explain the frequent absence of centripetal xylem in them.

The fructifications of the Lepidodendraceæ seem usually to have been cones; but Professor Bower in his latest book announces the forthcoming publication by Mr. Kidston of the description of a large tree-like type known as *Pinakodendron* in which the sporophylls are not disposed in cones, but in which the sporangia are associated with the ordinary leaves of certain portions of the stem (4). We do not as yet know if this fossil belongs to the Lepidodendraceæ; this, however, will be easily settled when Mr. Kidston's description appears, for the Lepidodendraceæ are sharply characterized by the comparatively simple anatomy of their stems

and the presence of a ligule. But as the *Lepidodendraceæ* are the only well-known dendroid Lycopods, and as they were certainly a dominant group in the middle Coal Measures, from which *Pinakodendron* comes, it seems probable that the latter belongs to this cycle of affinity.

The comparatively simple anatomy of the stem of the *Lepidodendraceæ* points them out, in spite of their great size, as a relatively primitive order, and the high specialization of their underground organs, the *Stigmariæ*, seems to preclude the idea of their having undergone any considerable reduction. For these reasons and on account of the want of differentiation between its leaves and sporophylls it seems preferable, pending the publication of Mr. Kidston's paper, to regard the non-strobiloid condition of *Pinakodendron* as primitive. But in by far the greater number of cases the fructifications were cones; sometimes these were undoubtedly borne at the ends of slender branches. Until quite recently it was held that they were sometimes also borne on the old stems; such forms were known as *Ulodendron*. Their stems bore the ordinary *Lepidodendraceous* markings—either of the *Lepidodendron* or of the *Sigillaria* type, but they also bore large roundish scars, usually disposed in two longitudinal rows; sometimes these scars appear to have been arranged quincuncially (14). They are slightly depressed structures, at the bottom of which is a small circular scar known as the umbilicus; the umbilicus is slightly excentric, being nearer the lower edge of the main scar, and from it slight ridges radiate upwards and outwards; the lower part of the scar bears spirally arranged dots. These *Ulodendroid* scars are usually interpreted as being the marks left by very big deciduous sessile cones, the umbilicus representing the very short peduncle, and the radiate markings being due to the pressure on the growing stems of the base of the large cone. Mr. Watson, however, has shown that this explanation is inadequate; he points out that these scars occur on the stem of *Bothrodendron mundum*, and that there is a very strong probability that the cones of this species were small structures borne on comparatively slender twigs (25). Unfortunately the connection between these cones described by Mr. Watson and *Bothrodendron mundum* is not absolutely proved, though it is very strongly supported by the constant association of the two structures and the close similarity of the wood in the axis of the cone to that of a small twig of *Bothrodendron mundum* (24). Mr. Watson maintains that the

largest definitely Lepidodendroid cone with the structure preserved known to him is *Lepidostrobus Brownii*; this cone is about one quarter of the size of the largest Ulodendroid scars (25). Graf Solms-Laubach, however, mentions various colossal cones (21); the details of their structure are unfortunately not known and they may not have belonged to the Lepidodendraceæ. In any case, as they appear to have possessed an axis of exceptional size, they could not very well have been attached to any *Ulodendron*-scar known to us, for the umbilicus or point of insertion of the supposed axis of the cone is invariably small. Mr. Watson points out that the shape of the Ulodendroid scars is inconsistent with the view that they increased secondarily in size after the cones had been detached. He regards the scars as formed by the attachment of branches and considers the umbilicus as the point of the stele of the branch; he asserts that this theory is supported by the arrangement of the markings on the scar itself, or at least on its lower part; these resemble the leaf-traces of the order. The unequal size of these dots, which it would be difficult to account for if they are regarded, as is usually done, as leaf bases, is explained by the fact that some of these departing leaf-traces would naturally be cut through tangentially. The similarity of these markings to Lepidodendraceous leaf-traces had already been commented on by Graf Solms-Laubach (21). Mr. Watson contends that the ill-defined structures, rarely found attached to the Ulodendroid scars, are not, as had been been supposed, cones. It seems very likely that his theory, if not completely satisfactory, yet comes nearer to the truth than the commonly accepted interpretation of the facts. It has the advantage of not supposing that such an ancient order as the Lepidodendraceæ had acquired a character, namely the production of cones on old stems, which on comparative grounds, and on account of its uniqueness, was probably not primitive. On the other hand Dr. Scott, in the final chapter of the first edition of his "Studies," remarks that the Palæozoic Lycopods were more specialized than their recent allies in the sharper definition of their strobili (*Pinakodendron* being then unknown) and he adds: "The frequent differentiation of the shoots on which the cones were borne (*e.g.*, the Halonial branches of *Lepidophloios*) is another indication of the same rule" (13). These Halonial branches seem to have been the ultimate ramifications of Lepidodendroid stems, and the scars which they bear were thought to be of the same nature as those of *Ulodendron*, though they were much smaller and usually spirally

arranged. The spiral arrangement was not, however, absolutely constant in *Halonia*, any more than the distichous one in *Ulodendron*, but this was commonly asserted to be due to the fact that the cones supposed to be borne on the scars of the latter were sessile, so that the bases of the lower sporophylls were supposed to be in contact with the stem, while the cones borne on the Halonial branches were regarded as being pedicillate. The fact that the appendages attached to the Halonial scar sometimes bore scales quite different from the vegetative leaves strongly supports the view that the axes attached to these scars were cones. But as Dr. Scott points out in the last edition of his "Studies," the doubts as to the nature of *Ulodendron* require that the structure of *Halonia* should be reinvestigated (14).

Passing to the consideration of the cones themselves, there is the well-known type of *Lepidostrobus*, undoubtedly representing a type of fructification borne by certain species of *Lepidodendron* and *Lepidophloios*. In *Lepidostrobus* each sporangium is radially elongated for a considerable distance and seated on the upper surface of the sporophyll; beyond the sporangium is the ligule and beyond the latter the distal end of the sporophyll turns vertically upwards (11). The structure of the fructification of *Bothrodendron* is only accurately known in one species, probably the cone of *Bothrodendron mundum*. As in *Lepidostrobus* the ligule is situated beyond the sporangium. The latter is borne on the upper surface of the sporophyll, but it is not radially elongated; indeed, it is more elongated longitudinally than transversely or radially. It is borne on a stalk, devoid of vascular tissue, and inserted on the horizontally expanded portion of the sporophyll (24). In *Spencerites* another cone, which though clearly Lycopodial, may or not be Lepidodendraceous, the sporangia are approximately spherical and inserted on a very small parenchymatous ventral projection of the sporophyll, to which they are attached by their distal ends. Miss Berridge has shown that beyond the sporangium the sporophyll turns vertically upwards (2). Besides these types of cone, there is that of *Sigillariostrobus*; this fructification was, as its name indicates, the cone of *Sigillaria*; its sporangia are radially elongated, though not nearly so much so as those of *Lepidostrobus*. If *Spencerites* does not belong to the Lepidodendraceæ (and this must remain an open question so long as its vegetative parts are unknown), it seems not improbable that the *Bothrodendron*-type of cone may be the most primitive within the order and that

Lepidostrobus and *Sigillariostrobus* were derived from a type with such approximately spherical sporangia, either by independent radial elongation of their sporangia, or by such elongation in the sporangium of their common ancestor, which was carried further in the evolution of *Lepidostrobus* than in that *Sigillariostrobus*. If *Spencerites* is a *Lepidodendraceous* fructification it may well be the most primitive type of all. The reasons for this are :

(a.) The distal attachment of the sporangia appears to be a primitive character (13), (17); it is unknown among recent Lycopods, but was characteristic of the Palaeozoic Sphenophyllales, the phylum to which the Lycopods, though very much isolated, are probably closest; and if a character occurs among the primitive forms of allied phyla, its presence may be expected in the primitive members of a given phylum. It is, however, quite possible that the ventral sporangiferous projection so reminiscent of the Sphenophyllaceous sporangiophore is not homologous with that organ, for it contains no vascular tissue. In this connection it should be noted that Miss Sykes has recorded the presence of lignified cells, not, however, in contact with those of the sporophyll-trace, in the sporangial stalk in other species of the phylum (23). She even contends that such cells, the existence of which is denied by Dr. Scott (14) and by Miss Berridge (2), occur in the latter's preparations of *Spencerites*. This argument, founded on the primitiveness of the distal insertion of the sporangium, and therefore on a theoretical assumption not universally admitted, is certainly a weak one; but it is to a certain extent reinforced by the fact that the sporangium of *Sigillariostrobus Crepini* is also attached to the sporophyll by its distal end; the appearance of such a character in another genus of the order favours the view that the common ancestor of the genera of the order may have possessed this feature. This cone also approaches *Spencerites* and *Bothrodendron* in the fact that it is not radially elongated. Unfortunately its attribution to *Sigillaria*, is not considered to be perfectly established (12).

(b.) The axis of *Spencerites* was in some cases destitute of a pith, and a solid stele is generally admitted to be more primitive than a medullated one. In cases where a pith is present it appears to be a small one (14), whereas the pith of *Lepidostrobus* seems to have been well developed, except at the apex of the cone (3), (11). This difference between *Lepidostrobus* and *Spencerites* is presumably partly due to the difference in the size of the two genera.

(c.) The only two species of *Spencerites* with which we are acquainted come from the Lower Coal Measures.

The principal objection to regarding *Spencerites* as the cone of a primitive member of the order, is that the evidence that it belonged to one of the *Lepidodendraceæ* is very weak. It seems clear that *Spencerites* was eligulate, and the presence of a ligule is characteristic of the leaves of all *Lepidodendraceæ*, with the possible exception of the doubtful *Archaeosigillaria*; it is also found in connection with the sporophylls of the better known forms; it has not yet been detected in *Sigillariostrobus*, though its presence there will probably be demonstrated, for it has recently been shown that the leaves of *Sigillaria* were provided with a ligule (1). Therefore the absence of a ligule in *Spencerites*, coupled with the distal insertion of the sporangium and other less important differences, seems to show that though this genus is presumably the cone of a fossil member of the *Lycopodiales*, it is probably not *Lepidodendraceous*. On the other hand the spherical form and distal insertion of the sporangium may well be primitive, and it might belong to some ancient eligulate type (such as *Archaeosigillaria*) closely allied to the *Lepidodendraceæ*.

Heterospory is presumably always evolved from homosporous, and the question thus arises whether this occurred in the case of the *Lepidodendraceæ* within the order, or whether the common ancestor of the order was already heterosporous. Well-marked heterospory has been found in all investigated species of *Sigillariostrobus* (except in the doubtful *S. Crepini* in which the spores are not known). Many species of *Lepidostrobus*, and all species of *Lepidocarpon* (to be considered presently) were heterosporous. The possibility of dioecism renders it almost impossible to be sure that any species is homosporous. Dr. Scott has recently asserted that it is almost certain that all *Lepidostrobi* were heterosporous, the two kinds of sporangia being borne on the same or on different cones (17). Dr. Scott thus maintains the heterospory of all *Lepidostrobi*, without calling in the help of dioecism. Only one kind of spore is known in *Spencerites*, but we possess so few examples of this genus that the presumption of homosporous thus afforded is weak.

Still the attachment and form of the sporangium are sufficiently characteristic to enable us to distinguish the cones of this

genus, and should further investigation reveal other homosporous cones, and no megasporangia, a fair presumption of homospory in *Spencerites* would be established. A homosporous condition would agree well with the relative primitiveness sometimes attributed to *Spencerites*.

Whatever the relationship between *Spencerites*, *Lepidostrobus* and *Sigillariastrobus* it is quite clear from Dr. Scott's work that *Lepidocarpon*, in which the megasporangia are retained on the cone until after the cavity of the megaspore is filled by the prothallus, was evolved from a heterosporous *Lepidostrobus*. The general anatomy of the axis and the structure of the cone are practically identical with those of *Lepidostrobus* (15). The principal differences seem to be that in the megasporangium only one spore-mother-cell underwent the tetrad division and that only one megaspore came to maturity; that the prothallus was developed while the spore was still enclosed in the sporangium, though no embryo has yet been found in this stage; and that the megasporangia and microsporangia were surrounded by an integument which grew up from the sporophyll; in the former it left a narrow radially elongated micropylar crevice at the top; in the latter the integument was much less developed. Of the two species of *Lepidocarpon* at present known one comes from the Coal Measures, and the other from the Calciferous Sandstone Series of Burntisland, at the very base of the Carboniferous system. That a case of such extreme heterospory as that occurring in the species from Burntisland should occur at so early a period makes it clear that heterospory must have originated at a very early geological epoch, and lends some support to Dr. Scott's view that all species of *Lepidostrobus* were heterosporous.

All typical *Lepidodendraceæ* disappear before the end of the Permian (21); but Graf Solms Laubach has described, under the name of *Pleuromeia*, some fossils perhaps allied to the order (22). Unfortunately *Pleuromeia* is only known as impressions and we are therefore ignorant of its anatomy. Dr. Scott has suggested that the four lobes found at the base of the stem of the *Pleuromeia* marked with scars left by roots may correspond to the four Stigmarian axes radiating from the base of the stem of *Lepidodendron* and *Sigillaria* (13). In its vegetative parts *Pleuromeia* agrees fairly well with the *Lepidodendraceæ* though the whole plant is on a smaller scale; the casts show that the stems were medullated, the leaves appear to have been small, simple and peculiar, parichnos appear

to be present (22); the fructification, judging from Graf Solms-Laubach's description, appears to have resembled that of the Lepidodendraceæ in so far that it was strobiloid (22). Professor Bower, however, regards the strobilus as undifferentiated from the main axis that bears it (4). Unfortunately the interpretation of the scales composing the fructification of *Pleuromeia* is very doubtful. In one case at least the scale seems to have borne on its back a small body, which Graf Solms-Laubach states one might feel inclined to term, as did Spieker, an earlier investigator, a sporangium or an ovule of the type found in *Araucaria* (22). Such an interpretation cannot be harmonized with the fructification of any of the known Palæozoic Lycopodiales—or indeed with any known member of the phylum,—especially as regards the insertion of the sporangium, if such be the structure borne on the scale. The details of the fructification are, however, so ill-preserved that it is quite likely that they have been misinterpreted; mention has therefore been made of the genus here, though its position is admittedly a very doubtful one.

The next order, that of the Isoëtaceæ, contains but the single genus *Isoëtes*. By far the greater number of species are amphibious or aquatic. Dr. Scott and Mr. Hill investigated *Isoëtes hystrix*, one of the two terrestrial species, and as a result of their researches it appears likely that the common ancestor of all the species of the genus was amphibious (18). Presumably, therefore, this habit was retained in the greater number of species, a certain number becoming modified in connection with an aquatic or sub-aquatic habit, and two adapting themselves to a terrestrial existence. The plant of *Isoëtes* is much stunted and bears closely set ligulate leaves, most of which bear a single sporangium on their upper surface. The stem has little primary xylem (which is apparently centripetal) and shows secondary growth in thickness; this is generally described as abnormal, for the cambium produces a small amount of xylem and phloem on its inner side and secondary cortical tissues externally. But Dr. Scott and Mr. Hill have found that in *Isoëtes hystrix* the cambium is sometimes at first normal in position with regard to the elements to which it gives rise; this method of secondary growth, *viz.*, the formation of xylem internally and phloem externally, is, however, soon replaced by the abnormal one. As this species has, owing to its terrestrial habit, better developed xylem than many others, it is possible that this normal form of secondary growth is primitive and that its very

general replacement by the abnormal kind is a later modification. On the other hand the secondary growth may have been primitively abnormal in the Isoëtaceæ, and the normal one may have arisen in connection with the demands for more secondary thickening in a terrestrial species.

The genus shows no other variations of great phylogenetic interest, so that we may proceed to consider the affinity of the Isoëtaceæ with the Lepidodendraceæ. Dr. Scott's comparison of *Pleuromeia* with the latter order has already been mentioned; in the final chapter of the first edition of his "Studies" we find the following interesting passage: "The curious Triassic genus, *Pleuromeia*, has much in common with *Sigillaria* and in some points appears to approach *Isoëtes*. The four Stigmarian axes which radiate from the base of the Sigillarian stem are in *Pleuromeia* replaced by four rounded lobes, separated by furrows and marked with the bases of roots. A further reduction might conceivably have led to the characteristic furrowed stem of *Isoëtes*. However, neither the inner structure of *Pleuromeia*, nor the nature of its reproductive organs, is known, so the question must remain *sub judice*" (13).

The arguments favouring the reduction of *Isoëtes* from the Lepidodendraceæ will now be stated and examined. Secondary growth in thickness of the stem of *Isoëtes* is a very significant character, for we are obliged to regard it as a survival in reduced forms, since the stunted nature of the plant and the probability that the terrestrial species are descended from an amphibious form preclude the notion that it might be a recently acquired character. If the normal kind of cambium is primitive *Isoëtes* may well have been descended from a typical *Lepidodendron*; if the abnormal secondary growth is primitive it is noteworthy that, although Dr. Scott and Mr. Hill found no exact parallel to this method of growth in any other plant, they expressed the opinion that among Lycopods it resembled most closely the type of secondary growth found in *Lepidodendron fuliginosum*. The absence of a pith may be due to reduction, but if *Isoëtes* is descended from the Lepidodendraceæ it may well have originated from primitive, protostelic forms with centripetal primary xylem, and though the stele was probably larger in the ancestors of *Isoëtes* it may never have been more complex. The presence of a ligule cannot be held to weigh heavily in favour of an affinity with the Lepidodendraceæ, for it is also characteristic of the herbaceous *Miadesmia* and

Selaginellaceæ. A remarkable similarity between the two orders is the presence of mucilage-containing cavities in the leaf-bases of *Isoëtes* and parichnos in the Lepidodendraceæ. In *Isoëtes* these arise by the degeneration of a strand of parenchyma and in their origin as well as in their position on either side of the vascular bundle they appear to be strictly comparable to the parichnos. They are, indeed called parichnos by Mr. T. G. Hill, their discoverer (7). This point is not perhaps of great importance, since though parichnos are best known in the Lepidodendraceæ they occur also in the Lycopodiaceæ. The relatively large size of the leaves may be due in part to the extreme stuntedness of the stem, but this cannot account for their actual size, which finds its nearest parallel, within the phylum, in the Lepidodendraceæ. The occasional mesarchy of the foliar bundles, especially towards the base of the leaf, also recalls *Lepidodendron*, but this character is also found in herbaceous Lycopods and may, in this case, be due to the size of the leaves. The morphology of the Stigmariæ, or underground organs of the Lepidodendraceæ, and of their appendages has been much discussed. It is still an open question whether the main axes of *Stigmaria* are really represented by the lobes of the Isoëtaceous stem, but such an exceptional character as the downward growth of the base of the stem may indicate that the lobes were once, in the phylogeny, capable of distinct growth in a contrary direction to the normal upward growth of the stem. If *Isoëtes* arose from the Lepidodendraceæ, the Stigmarian axes must have been reduced, in the course of its evolution, almost to disappearance. But in any case, in a phylum such as the Lycopodiales, where root and stem are admittedly not sharply differentiated from one another, the comparison between the roots of *Isoëtes* and the appendages borne by *Stigmaria*, a comparison that has been strongly emphasized by Dr. Scott in a course of lectures delivered in 1904, seems a legitimate one. Both are monarch dichotomously branching subterranean organs. The agreement between them is striking, for monarch roots are rare, though they occur within the phylum in *Selaginella*. The radial elongation of the sporangium of *Isoëtes* is certainly suggestive of *Lepidostrobus* and more particularly of the allied *Sigillariostrobus*, for the degree of elongation of the sporangium corresponds more nearly to that found in the latter. Though this character carries a good deal of weight, it should be remembered that radial elongation was not characteristic of all Lepidodendraceous sporangia, for those of *Bothrodendron* and of

Spencerites were more or less spherical, and as shown in the above discussion this spherical form of sporangium was probably primitive for the order. Professor Bower, who was the first accurately to compare the sporangia of *Lepidostrobus* and of *Isoëtes*, and who favours the view of the reduction of the latter from the Lepidodendraceæ, has pointed out the resemblance between the trabeculæ that render the sporangium of *Isoëtes* incompletely septate and certain sterile plates of tissue found in the sporangia of *Lepidostrobus Brownii* (3). It is true that he was unable to prove a connection between the sterile plates and the upper sporangial wall of the fossil, and as the sterile bands extend upwards from the sub-archesporial pad they may only be out-growths from it, and not formed, as they are in *Isoëtes*, by the sterilization of potential sporogenous tissue. The point is not quite proved, but the available data incline one to the view that the structures are strictly comparable in the two genera, though they may, even so, have arisen independently in response to a demand for better nutrition of the spores, consequent on the radial expansion of the sporangium. The velum of *Isoëtes* offers at best a poor analogy with the integument of *Lepidocarpon*, for in *Isoëtes* the velum, when present, appears to arise distally, whereas the integument of *Lepidocarpon* originates chiefly from the sides of the sporophyll. The velum is moreover very inconstant in *Isoëtes*, being present poorly developed, or absent in closely allied species. A character of minor importance, but suggestive when combined with so many other indications of affinity, is the persistence of the leaf-bases on the stem after the lamina has withered.

The arguments against the reduction of *Isoëtes* from the Lepidodendraceæ include three of considerable importance. The first of these is that the central cylinder of the stem of *Isoëtes* has been described by Professor Farmer as having no truly cauline part (6), whereas the cauline part of the stele is well-developed in the Lepidodendraceæ. Dr. Scott and Mr. Hill, however, after a thorough investigation of the anatomy of *Isoëtes hystrix* concluded that this was not so in the mature stele of that species (18). They point out that it is arbitrary to regard the stele as entirely built up of leaf-traces when it is manifestly impossible to refer all its constituent elements to the particular leaf-trace to which they belong, and they quote Professor Farmer's admission that the distinction lies rather in the mind of the investigator than in the stele itself. It is probable that at least in the terrestrial species with their better

developed xylem, a part of the cylinder is purely caulinè ; but even if Professor Farmer's view of the nature of the stele of *Isoëtes lacustris* were made to apply as a generalization to the rest of the genus it would not invalidate their origin from the Lepidodendraceæ, since if the latter supposition be correct extreme reduction of the stem must have taken place, and this must obviously have affected the size of the stele considerably ; the leaves, probably, were also reduced, though not nearly to such an extent as the stem, and their bundles, therefore, carry away a comparatively larger portion of the stele of the stem, so that the purely cauline portion of the latter might well become obsolete.

This leads us to the second and more serious objection to the hypothesis under discussion : the extreme reduction which it supposes and the absence of any intermediate forms, except the doubtful *Pleuromeia*. The anatomy of the latter is unknown, though judging from the figure given by Potonié its external appearance is somewhat similar to that of a *Sigillaria* (12). Further, though Dr. Scott states that the nature of the reproductive organs of *Pleuromeia* is not known, such doubtful indications as the fructifications afford agree neither with the Lepidodendraceæ nor *Isoëtes*. *Pleuromeia*, then, somewhat resembles *Sigillaria* in appearance and is intermediate in age between the latter genus and *Isoëtes*, but it has not been shown to be intermediate between them in any essential character. The reduction is then very great, for, whereas most Lepidodendraceæ were trees, bearing numerous well-developed leaves, Dr. Campbell considers that in *Isoëtes* all the leaves were sporophylls, except those imperfect ones separating the sporophylls of successive years (5). As he calls these sterile leaves imperfect he presumably regards them as sporophylls sterilized by unfavourable conditions. Their position would agree with such a hypothesis, but if this interpretation is correct the vegetative leaves of the Lepidodendraceæ have been reduced until they became obsolete. The amphibious mode of life, hypothesized for the common ancestor of all the species of the genus, and the aquatic habit of many recent species may, however, account for a considerable amount of reduction.

The third objection to the origin of *Isoëtes* from the Lepidodendraceæ is the fact that it is non-strobiloid while most of the latter appear to have possessed very definite strobili. In *Pinakodendron*, however, the sporophylls were not differentiated from the leaves, and were not aggregated into cones ; should this genus

prove, on the publication of Mr. Kidston's description of it, to have Lepidodendraceous affinities, it may turn out to be close to the direct ancestor of *Isoëtes*. Thus, even if descended from the Lepidodendraceæ, *Isoëtes* may be primitively non-strobiloid, but, on the whole, if we admit the excessive reduction outlined above we shall find no difficulty in regarding its non-strobiloid condition as due to reduction.

It will be seen that this question of the origin of *Isoëtes* by reduction from the Lepidodendraceæ in the widest sense of the word is not yet solved, but in the present writer's opinion there is a strong probability that it should be answered in the affirmative.

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THE MEANS OF DISTRIBUTION OF HEPATICÆ.

BY HENRY R. YEATES.

IN the issue of "The New Phytologist" for October, 1907¹ Professor Campbell argues that one of the most important means of arriving at the antiquity of any group of organisms is the study of the present distribution of the group and the means of distribution in recent times. This aspect of the subject has for a long time been uppermost in the writer's mind, and has been strengthened by the local distribution of those genera which are common in our own country. With such hygrophilous plants as Hepaticæ, built up entirely of cellular tissue and ill adapted to survive prolonged periods of drought, their migration is largely limited to those areas which afford means for water carriage. Every botanist who has made a practical study of the distribution of Hepaticæ, in any one area, is well aware that they are the occupants of the low-lying valleys, where moisture is abundant; and when met with in more elevated districts the geological formation is such as to connect the station with some valley not far remote.

Certain genera, from the greater delicacy of their tissues, not only require a superabundance of water, but also a comparatively high thermal constant for the maturation of their spores, and are unable to persist in regions where there is abundant evidence of their having formerly flourished. *Reboulia hemispherica* and *Dumortiera irrigua* have all but disappeared from our English representatives, and though at the present day occurring sparsely in one or two isolated stations, their organs of fructification are rarely met with in the mature state.

Professor Campbell is quite right in discounting the too prevalent assumption that because of the lightness of the spores of Hepaticæ they are specially fitted for the rapid dispersal by wind. The writer's experiments with the spores of *Fegatella conica* and those of other genera are in perfect harmony with those undertaken by Mr. H. B. Humphrey, cited by Professor Campbell² and the conclusion he has arrived at is that not only do these bodies quickly lose their power of germination owing to dessication, but that no important number of them ever germinate at all, owing to unfavourable conditions surrounding the parent structures. Under

¹ D. H. Campbell. On the Distribution of the Hepaticæ and its Significance, *New Phytologist*, Vol. VI., p. 203.

² l.c. p. 210.

these circumstances little credence can be given to the supposition that the present distribution is due to the dissemination of spores through the agency of wind. Moreover, in many dioecious species the production of spores appears to be on the decline. The writer has frequently found patches of *Metzgeria furcata* composed entirely of female plants and although perfectly developed calyptras were present, these, upon microscopic examination, were found to contain only masses of disintegrated matter. Whenever the mature sporophyte has been met with, the plant bearing it has been associated with others of the male sex. This circumstance seems to point to the conclusion that *Metzgeria* cannot produce spores parthenogenetically. One other circumstance has struck the writer very forcibly, and that is the very great variation in the yield of antheridia by *Metzgeria*. In 1904 the yield was exceedingly prolific, in the succeeding year at the same season hardly an antheridium could be found. The present dispersion and distribution of *Metzgeria furcata* cannot possibly be due to the sexual act; but is solely due to the production of thallidia and the ease with which they are detached from the parent structure by mechanical agencies. The attachment of the marginal thallidia to the parent structure is so slender that they are readily separated by currents of water and conveyed from higher to lower levels on the same tree trunk and from one tree to another when the circumstances of environment are suitable. In this way the writer is able to account for the presence of *Metzgeria* being more prevalent on the trunks of trees at the bottom of wooded glens than upon those higher up on the flanks on either side.

The widespread tropical genus *Dumortiera irrigua* has a very limited distribution in Europe. It occurs only in this country in Devonshire, and very sparingly in Fairlight Glen, Hastings. At each of these stations the plants occupy specially ideal situations both as regards shelter and shade and where the water constantly drips from overarching rocks. The writer has had the plants at the Hastings station under periodical observation for some years but has failed to meet with the sexual organs in a mature state. They reach a certain stage of development and then drop off. In 1906 Dr. A. Gepp showed the writer specimens bearing mature female receptacles which had been procured in Devonshire. If, however, the writer's information is correct, the production of mature sexual organs, so far as the plants in this country are concerned is a matter of rare occurrence.

Dumortiera irrigua is again met with sparingly in the South-West of Ireland near Sorc Fell. Since the plants belong to a widespread tropical genus, this fact seems to indicate that they owe their present distribution to Miocene and Pliocene times when Great Britain and Ireland were united and when the climate especially during the earlier Miocene age must have been of a tropical character. Unlike *Fegatella conica*, *Pellia* and *Aneura*, which are so constituted as to survive great cold, the greater delicacy of *Dumortiera irrigua* seems to point to the necessity of a much higher thermal constant for its perpetuation. The same observation would seem to apply to *Marchantia polymorpha*, *Blasia pusilla* and *Lunularia cruciata*, which are by no means so evenly and widely distributed as is generally supposed. *Marchantia polymorpha* being more hygrophilous than *Lunularia cruciata* is unable to migrate far from the vicinity of running water. The writer has never found it growing in situations where the water supply was limited to the rainfall, nor in ditches which are intermittently wet and dry. Like *Metzgeria furcata* the male oophyte appears to persist to a greater extent than the female, and is more widely distributed. The plants grow together in matted groups on the shaded side of rocks which form channels for comparatively pure water and not far removed from the normal water line so as to be ensured against dessication.

Lunularia cruciata, unlike *Marchantia polymorpha*, has a wide distribution, not being confined exclusively to water courses, but is found growing in isolated patches in very diverse situations. The writer has found it growing upon boulders occupying deep seated valley-beds, upon stiff clay loams forming the banks of roadside water channels, at the bottom of old walls and outhouses, and upon shaded banks often hidden from view by overhanging brambles. This wide distribution of *Lunularia cruciata* is in no sense due to spore dissemination. The sexual activity so far as British representatives are concerned has declined to such an extent that the spore-bearing organs are now only met with in more Southern latitudes. Dr. A. Gepp however showed me a specimen of the fully developed sporophyte which had been produced by culture in a greenhouse.

The writer has occasionally met with specimens of the female oophyte in which archegonia were present, but never with the mature sporophyte bearing spores. Since however the organ has been produced under the more even temperature of a green-house and is still produced upon plants in more southern latitudes, we

may reasonably infer that our present representatives are of ancient origin and have come down to us from the Miocene epoch.

The distribution of *Marchantia polymorpha* and of *Lunularia cruciata* is to be explained by the asexual production of gemmæ and the ease with which these bodies are transmitted from place to place by mechanical agencies. To all intents and purposes they function as seeds, and to their agency is to be attributed the reappearance of plants in spring at those stations, from which they temporarily disappeared during the winter. This conclusion was forced upon the writer some three years ago after keeping observation upon the growth at various stations, which led him to make experiments. A number of gemmæ were removed in the late autumn from the parent structure and planted in brick-work crevices at the bottom of a damp wall in the writer's garden, with the result that in the following spring he had quite a crop of *Lunularia*. These bodies, coated as they are with adhesive mucilage, not only become readily attached to the coats of animals and are conveyed from place to place, but retain their vitality through the winter. This view will account for the presence of *Lunularia* in those situations more or less frequented by rats, as in the neighbourhood of gullies, sewers, &c. as well as in the more open situations to which the gemmæ may have been conveyed attached to the feet of birds.

The multiplication of *Lunularia cruciata* by gemmæ during the early spring and summer is extremely rapid. Often two or even three cupules may be seen on one and the same thallus, and since the horns of the semi-lunar cupules are directed towards the apices of the plants, the gemmæ when mature, are guided outwards and downwards to new unoccupied soil. This circumstance accounts for the thickly matted clumps occurring so rapidly in the neighbourhood of isolated plants during the early summer months, whilst the migration of birds will account for its distribution in widely separated areas.

Fegatella conica, belonging to the Marchantiaceæ, and *Pellia epiphylla*, belonging to the thalloid Jungemanniaceæ, surpass in robustness the genera hitherto dealt with and seem to be quite at home in their British stations. They both are able to complete their life-cycles annually and are widely distributed. *Fegatella conica* is met with in great profusion in the counties of Kent, Sussex and Surrey, occupying the banks of the upper courses of the Medway and Rother and the many streams and brooklets feeding

these rivers. At Lamberhurst it occupies the lower facings of the sandstone bridge which spans the River Teise and just before reaching Battle it is found occupying the sandstone escarpments by the roadside. At Ecclesbourne and Fairlight Glens, Hastings, it is found fruiting regularly in April. The plants however growing on the banks of the rivers do not fruit periodically except in those situations where they are not liable to prolonged submersion during periods of flood, such as upon arches bridging streams. From the fact that *Fegatella conica* and *Pellia epiphylla* are found so extensively lining water courses and rarely elsewhere we may reasonably conclude that they owe their present distribution entirely to water carriage, not only of spores, but also of detached plants during periods of flood. We may also conclude that since these plants are able to complete their life cycle annually under the present conditions of our climate they have a greater chance of survival with us than *Dumortiera* and *Lunularia*, which show a waning sexual activity.

ON THE MEANING OF THE VARIOUS FORMS OF THE
MALE GAMETES IN THE PINES AND ALLIED
CONIFERS.

BY E. M. CUTTING, M.A., F.L.S.,

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IN 1892 Strasburger (17) described two unequal male cells as the product of division of the body cell in *Pinus sylvestris*. Each of these cells was surrounded by a very small amount of cytoplasm. As one would expect from the above description, and as Strasburger clearly shows in his figures 43 and 44, not only the cells but also the nuclei are of slightly different size. In 1894 Dixon (7) in describing the male nuclei of *Pinus sylvestris* speaks of them as being of about the same size, evidently meaning to suggest by this that, as far as he could see, they were not quite equal, but very nearly so. In his figures showing this dissimilarity the nuclei are situated in the upper part of the pollen tube, that is to say the inequality is present at quite an early stage.

Professor V. H. Blackman in his paper of 1898 (1) makes no reference to the relative size of the nuclei, but he has informed me that in one of his sections he remembers seeing two quite similar male nuclei and that they were situated very low down in the nucellar tissue just above the archegonia.

Coulter in 1897 (5) reported the existence in *Pinus Laricio* of two similar male cells containing two equal sized nuclei¹, and Chamberlain (2) in 1899 confirmed this. In 1901 Miss Ferguson (8) made a comprehensive study of the male apparatus in *Pinus Strobilus*, *P. austriaca* (which is merely a variety of *P. Laricio*), *P. montana* var. *uncinata* and *P. rigida*. Working with these she was unable to agree completely with any of the previous workers. In every case two unequal male nuclei were formed, but these remained embedded in one naked mass of protoplasm, no wall being formed between them.

In some serial sections of *Pinus sylvestris* ovules, prepared for demonstration purposes, I have observed several pollen-tubes containing male nuclei, and in all these cases there was only one cell, and enclosed in this two unequal nuclei. The smaller nucleus was directed towards the micropylar end of the nucellus, and in some cases lay quite close to the boundary of the protoplasm of the cell. The difference in size of the nuclei was more marked in those pairs which were near the archegonia than in those which were near the top of the nucellus. I am inclined to interpret this observation, as Miss Ferguson did in the case of *Pinus Strobilus* (8), that is to say that in their journey down the nucellus the difference between the nuclei gets more and more pronounced. The instance noticed above, when Professor Blackman found equal male nuclei quite near an archegonium, seems to be against this view, and suggests that *Pinus sylvestris* presents a state of affairs intermediate between *Pinus Strobilus* (8) and *Pinus Laricio*, as described by Coulter (5), forming at one time equal and at another time different grades of dissimilar nuclei. That is to say, if one regards the form with the equal nuclei as more primitive than the one with the unequal, *Pinus sylvestris* is a transition form from one state to the other.

There seems to be no *a priori* reason against one species of a genus having equal male nuclei while another species has unequal. Indeed, such a case has been recorded in the genus *Cephalotaxus*,

¹ Coulter's figure showing the pollen tube in this condition is reproduced in Strasburger's Text Book of Botany, 3rd English Edition, 1908.

in which one species, *C. drupacea*¹, has equal male nuclei, and another species, *C. Fortunei*, unequal.

Although Coulter has described equal male cells in *Pinus Laricio*, Miss Ferguson has recorded the existence of unequal male nuclei in *Pinus austriaca*, which I find is now regarded merely as a variety of *P. Laricio*. It is scarcely likely that a variety of any one species would agree in this respect more closely with other species than it does with the species of which it is a variety. Moreover Strasburger in his "Die Befruchtungsvorgänge bei den Gymnospermen," says that many pines behave as does *Pinus sylvestris* and amongst them he mentions *P. Laricio*. It will be remembered that Strasburger figures unequal nuclei in the former species, and, therefore, it seems more than likely that he intended it to be understood that *P. Laricio* had unequal male nuclei also. Coulter and Chamberlain also say that two male cells are formed in *Pinus Laricio*, but Miss Ferguson says of *P. Laricio*, as well as of the others she has examined, that although two male nuclei are formed, they remain in the same cell. Two species of one genus, *Torreya*, have been described, one with two male cells (Coulter and Land on *Torreya taxifolia* 6 and one with two unequal male nuclei in a single cell (Miss Robertson's *T. californica*, 15). But one would certainly not expect so great a difference as this in a variety, especially as other species agree with the variety. I do not, therefore, think that these observations of Coulter and Chamberlain are confirmed by more modern researches. *Pinus sylvestris* I therefore regard as falling into line with the other pines as they have been described by Miss Ferguson (8). Professor Blackman's isolated instance of equal male nuclei in *P. sylvestris* is probably a reversion to the time when equal nuclei were formed.

There can be little doubt that the body cell divided primitively into two equal male cells, and that the inequality of the male cells of such Conifers as *Cephalotaxus Fortunei* and *Torreya taxifolia*, and the inequality of the nuclei with the loss of the power of forming the two cells, as seen in the pines, *Picea* (Miyake 14), *Abies* (Miyake 13), &c., are recently acquired characters. Strasburger in 1892 suggested that these inequalities of the sizes of the cells (he was not aware of the cases in which no division of the cytoplasm was made between the two male nuclei) were due to the fact that in those cases only one male nucleus from one pollen grain has a

¹ Lawson (11) records equal male nuclei in *C. drupacea*, but his figure 27 shows unequal nuclei.

chance of fertilizing an archegonium; and since his paper many other investigators have remarked that in those cases in which both the nuclei in the pollen tube have an opportunity of fusing with an egg-nucleus, two equal male cells were differentiated, while in the cases in which only one nucleus could fertilize an archegonium either unequal cells or unequal nuclei were formed (11), (4), &c.

This reduction of the male cells seems to me to be connected with the differentiation of a smaller number of archegonia. When the latter are numerous, as in *Juniperus* or *Sequoia*, they are more likely to be situated near each other, and this would necessarily offer greater chances of both male nuclei fertilizing an archegonium, while, when the archegonia are few they are scattered and offer less or no opportunity. One pollen tube comes thus to be restricted to one archegonium, and, as a response to this, the male cells and nuclei are differentiated as to size, the larger being the effective one in fertilization. As a further reduction we get the stage in which the division of the male cell is omitted, although two male nuclei are still formed¹. From this point of view it follows that the reduction in the male apparatus follows the reduction in the female, and is not coincident with it. A conifer with a few archegonia might therefore still possess equal male cells if the habit of forming few and scattered archegonia had only recently been acquired in that form.

Several conifers exhibit a great variety in the number of archegonia formed. *Taxus baccata* is a very good instance of this. It usually forms about five to eight archegonia, but Jäger has reported as many as eleven, and Miss Robertson has even recorded seventeen. The latter writer also says that two archegonia sometimes occur without any intervening prothallial cells. *Taxus* therefore connects the *Pinus*- with the *Sequoia*- and *Juniperus*-type, both in the numerical variations of the archegonia and the occasional non-development of prothallial tissue between adjacent archegonia.

An unpublished observation of Professor Blackman's on *Pinus sylvestris* seems to me to have some bearing on the question of a wider distribution of archegonia on the prothallus. A few

¹ This latter state might sometimes be reached by passing through a stage in which equal male nuclei were formed, but only one cell (compare *Cephalotaxus drupacea*). One would however expect any reduction first to find expression in the nuclei, for the nuclear division precedes the cell division.

cases were observed in which the pollen-tube, instead of growing straight through the nucellus to the archegonia, made its way along the side of the prothallus, and having gone some distance in this direction then turned in towards the prothallus. This is strikingly like the state of affairs which Lawson has described for *Sequoia* (12), and without intending to suggest that this points to any very close relationship between *Sequoia* and *Pinus*, I yet think that it strengthens the view that the ancestors of the Pines at one time possessed a wider distribution of archegonia than they do at present. It may be noticed that the division and subsequent developmental history of the products of the division of the central cell of the archegonium suggests a series parallel with that of the division and history of the products of the body cell of the pollen-grain.

If the above theory of the cause of the inequalities and variations of the male apparatus of the conifers be accepted, it will be seen that these variations are connected with changes in the female apparatus. Goebel (9) has already suggested that the differences to be observed in the germination of Cycadean and Coniferous pollen-grains are connected with the structure of the ovule. It would therefore seem that the male gametophyte is comparatively plastic and liable to vary with changes in its environment, and a certain amount of caution is required in using data gained from it in discussing the phylogeny of any particular group.

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REVIEW.

PLANT PHYSIOLOGY AND ECOLOGY, BY FREDERIC EDWARD CLEMENTS, PH.D., *President of Botany in the University of Minnesota*. 315 pages, 125 Illustrations. London, 1907.

PROFESSOR CLEMENTS is one of the clearest and most logical exponents of ecology, and any contribution to the subject by him is worthy of earnest consideration. A great deal of the substance of the work now under review has already appeared in his "The Development of Vegetation" (1904) and also in his "Research Methods in Ecology" (1905). The latter work was reviewed in these columns at some length by Dr. F. F. Blackman and Mr. A. G. Tansley.¹ The present text has been largely based on the two earlier works, though most of the matter is new or re-written, and, to a fairly large extent, re-arranged. The plant is first considered as an individual, with respect to factor, function, and form, and then as a member of a plant group. "The book is intended for use with classes in second-year botany in College and

¹ NEW PHYTOLOGIST, Vol IV. 1905.

University, with the students of which classes it is possible, the author believes, to accomplish all the work set out in the book " in a course requiring six to eight hours of laboratory time each week." In our opinion, however, the author's ideas of the capabilities of such students reflect his unbounded enthusiasm for his subject. " A bibliography has not been deemed necessary and has not been given," but it is a pity, we think, that there are no references to original memoirs.

The first eight chapters deal respectively with such questions as Stimulus and Response, The Water of the Habitat, Adjustment to Water, Adjustment to Light, Adjustment to Temperature, Adjustment to Gravity, Contact and Shock, Adaptation to Water, and Adaptation to Light. It will be seen that these are matters which are usually left to the plant physiologist. The author has stated elsewhere his reasons for regarding ecology and physiology as essentially identical; and in his preface to the present work he anticipates a possible objection that since ecology and physiology are here blended, it is impossible to give to either what would be regarded as a complete treatment by a specialist in either line. Though the author states he has made no attempt to touch all the points in each, he thinks that nothing fundamental has been omitted. Whether or not we agree with this view depends on our views of what is fundamental to physiology. For ourselves, we regard respiration as distinctly fundamental, and we cannot think that this aspect of physiology has received in this text-book, the attention which its importance demands. In fact, we feel that it is an aspect of physiology which does not lend itself to adequate treatment by the author's general method of study. It is true, indeed, as Professor Clements maintains, that much of the observational and experimental physiology of the laboratories has, in the past, been pathology; and although pathology is a necessary study we are unable to agree that it is desirable to introduce it into courses of elementary physiology, and Professor Clements will have rendered an inestimably high service to botany if he initiates, as in this work he endeavours to do, a study of precise observations and experiments of the functions of plants in their normal habitats. We seriously doubt, however, if the course of study outlined in the present work is either practicable or desirable in the case of students who are not already acquainted with the experimental study of the functions of normal terrestrial plants. If the author had written his book for such students, he could, without fear of criticism, have omitted much

matter which he has felt compelled to insert—matter, we mean, which can only be held to be ecological when such a broad view is taken of ecology that the term ceases to possess any precise or definitive significance. In short, whilst it is self-evident that physiology and ecology have much in common, and that many physiological experiments should be conducted in the field, we do not believe that it is in the interests of either of these branches of botany to blend, at the present juncture, a text-book of physiology and one of ecology. We should, however, welcome a text-book which dealt with ecology from the physiological point of view, and which was written for students who had already received some training in the methods of plant physiology.

In studying the various factors of the habitat, the methods put forward by Professor Clements are essentially quantitative. Such a plan is excellent so long as the right things are measured, but this cannot be said of all the quantitative methods detailed in the book. For example, the method of obtaining soil-samples (p. 10) gives no guarantee that the soil examined is the soil being put to use by the plant which is being investigated. It may be admitted that practically all agriculturists make the same mistake. Soil analyses rarely, if ever, take into account the facts that different species of plants utilize different layers of soil, and that these different layers of soil possess different water-contents and different mineral-contents. An analysis of "a soil" is not of much consequence; what matters is an analysis of that part of the soil in which the roots of the plants are functioning.

Again, in determining the amount of available water in the soil, the whole method turns on the recognition of the time "when the plant wilts completely." Such a determination is not difficult in the case of plants with thin deciduous leaves which contain much water, such as *Helianthemum* and *Dahlia*; but it is more than difficult, it is impossible, in the case of many plants with small, dry, evergreen leaves such as *Calluna* and *Erica*, which die before they wilt. Even in the case of some plants with thin deciduous leaves, after the leaves have wilted completely, the work of transpiration and assimilation is continued by the young shoots, as in *Vaccinium Myrtillus*. In all such cases, and perhaps also in the case of such plants as *Sedum* with succulent leaves, the method of Professor Clements breaks down. Generally, we think that a number of the quantitative experiments here outlined possess only a *quasi*-exactness which however may deceive the unscientific.

A chapter is devoted to experimental evolution, namely to The Origin of New Forms. Without doubt, students should be required to attack this subject by the method of experiment, but the only experiment specifically detailed by Professor Clements should, in our opinion, be utilized by other authors as the way in which the subject should *not* be studied. We give the directions for the experiment in the author's own words:—

“Experiment 58. The occurrence of new forms in nature. Make a careful scrutiny of the species of the flora for the purpose of discovering ecads, variants, mutants, and hybrids. Note the differences between the parents and the new forms discovered. Estimate the chances the new forms have of surviving, using number, vigor, kind of modification, etc., as a basis for this.”

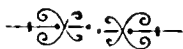
Second-year students of American Universities must be vastly superior to their British confrères if they are fit to be entrusted with “an experiment” of this character! Seriously, the observations and experiments necessary to carry out an investigation of this nature can only be performed by a botanist who has had many years' experience of practical physiology, ecology, and taxonomy. The “careful scrutiny” necessary to establish the claims of a single natural ecad, variant, mutant or hybrid demands observations and experiments which must be carried on through more than a single year. Such observations and experiments are of the nature of a research which may fittingly be entrusted to picked advanced students; but whilst we strongly desire to see a great increase in the number of such researches, we think that any attempt on the part of average second-year men to perform “experiment 58” would end in unmitigated disaster.

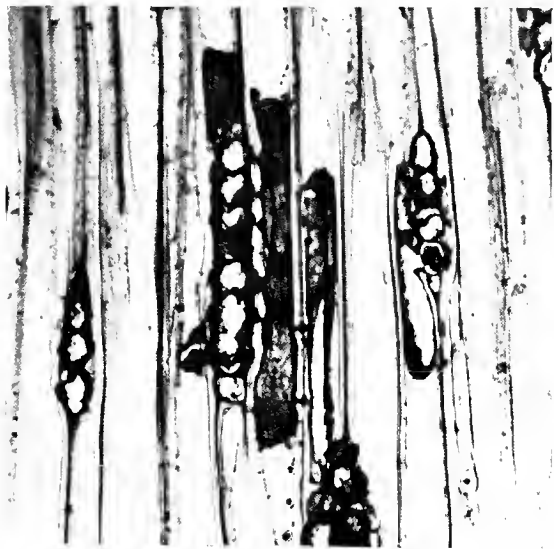
The remainder of the book deals with matters which are more strictly ecological. After an introductory chapter on Methods of Studying Vegetation, there follow chapters on The Plant Formation, Aggregation and Migration, Competition and Excess, Invasion and Succession, and Alternation and Zonation. Professor Clements' treatment of these subjects is well-known to ecologists, and the prevailing judgment of British ecologists at least is that his treatment is clear, definite and precise. However, all the author's views have been previously given in his Research Methods; and the *raison d'être* of Plant Physiology and Ecology is that the methods are set out for use by students. Judged then as a students' text-book, we cannot regard the work as a success, and we do not anticipate its general adoption in College and University classes. We should greatly like to see a text-book of practical ecology for students; but such a text-book, if it is to be a success, must be

more practicable than the one before us: it must set out more experiments, and the experiments must be of a simpler and yet more rigid nature: there must be less matter in the book, and this matter must be set out in a less didactic and more judicial manner. As an example of the somewhat dogmatic attitude sometimes adopted by the author, we may quote the following:— “It now appears to be entirely incorrect to ascribe the presence or absence of certain species on limestone soils to the chemical nature of the latter” (p. 18). It is interesting to compare this dictum with another from Schimper’s *Plant Geography* (p. 101, English edition):— “The ‘chemical theory’ has now been indisputably maintained, being supported by a correct apprehension of the problem, as well as by better material from field observations, by analyses of soils, and by cultures.”

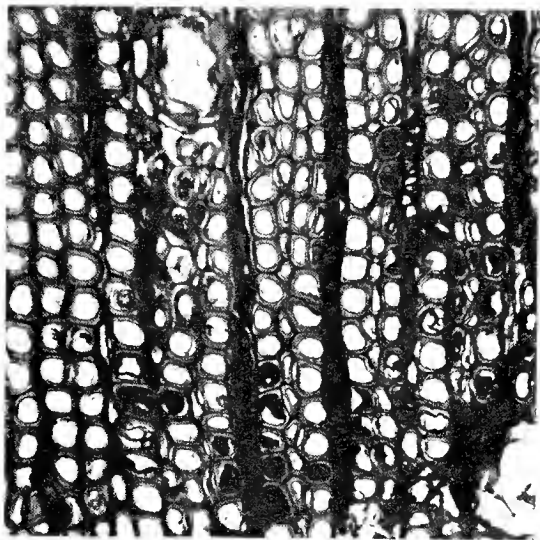
We hope that this rather adverse criticism of Professor Clements’ text-book will not be interpreted as an adverse criticism of his system of ecology as detailed in his other works and memoirs. Professor Clements’ philosophical outlook on ecology as a whole and on its relations to other departments of botanical science, his persistent advocacy of exact and quantitative work, and of the necessity of carrying experimental physiology to the natural plant habitat stamp him as one of the greatest ecologists of the age, and will leave an impress on ecological thought and ecological methods which will be felt for many generations to come.

C. E. MOSS.

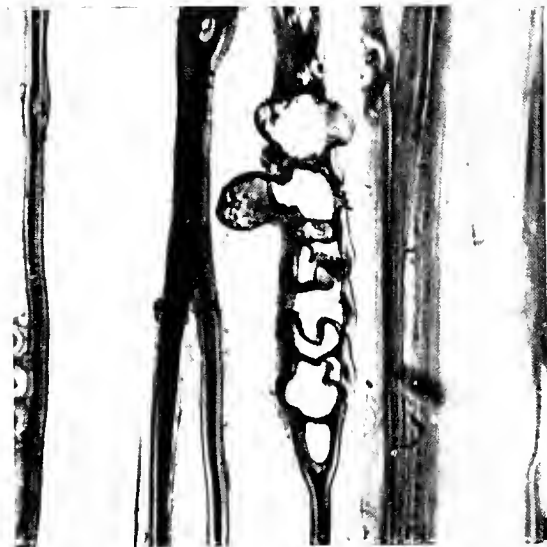




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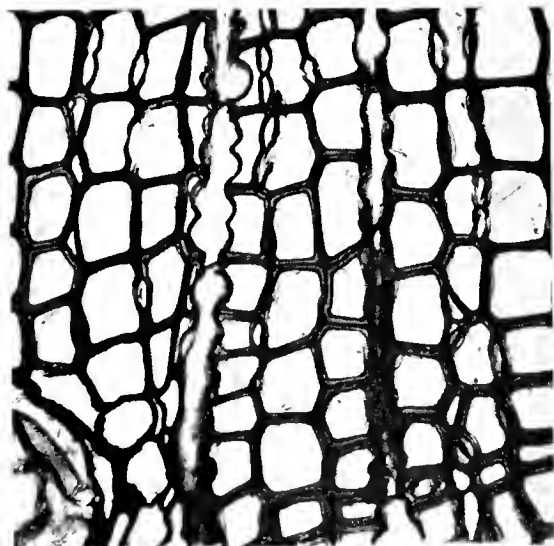
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THE
NEW PHYTOLOGIST.

VOL. VII., No. 8.

OCTOBER 31ST, 1908.

THE PHYLOGENY AND INTER-RELATIONSHIPS OF
THE PTERIDOPHYTA.

BY LADY ISABEL BROWNE.

IV.—THE LYCOPODIALES (*continued*).

SELAGINELLACEÆ AND LYCOPODIACEÆ.

Selaginella is the only existing genus of the Selaginellaceæ, but Professor Halle's and M. Zeiller's recent researches have cast light on certain heterosporous herbaceous Palæozoic Lycopods, formerly known as *Lycopodites*. These forms, now called *Selaginellites*, though only known as impressions, appear to be very close to *Selaginella* and ought probably to be included in the same order as the latter. *Miadesmia membranacea*, recently fully described by Miss Benson, appears to belong to the same cycle of affinity, though it shows certain characters peculiar to itself.

The most primitive type of stele found in *Selaginella* is presumably the protostele of *S. spinosa*. The creeping axis of this species contains an endarch and the erect stem an exarch protostele. Professor Harvey Gibson, in 1894, selected *S. laevigata* var. *Lyallii* (a highly complex species which may, in places, possess as many as thirteen steles) as exhibiting the most primitive type of stelar anatomy and sought to derive the protostelic *S. spinosa*, as well as the other types of stele occurring in the genus, from such a type. At that time, however, the primitiveness of the protostele was not as widely accepted as at the present day; but though most botanists would probably accept the primitiveness of the protostele of *S. spinosa* the case in favour of the exarch protostele being more primitive than the endarch one is not so clear. The complete absence of centripetal xylem in the creeping axis of this species is a strong argument against the primitiveness of exarchy. But there is good reason to believe that among the Ferns spiral vessels, representing true protoxylem, tend to disappear when the growth of the axis has,

in the phylogeny, become very slow, and there is some evidence that should the plant's descendants revert to a more rapid growth in length the protoxylem may reappear in a different position. There is no positive evidence that this has occurred in the creeping stem of *S. spinosa* and the analogy suggested is with a very remote group of plants. The creeping axis of *S. spinosa* might be compared to such of the Stigmarian axes as possess only centrifugal xylem; but the cases are not strictly comparable, for in the different species of *Stigmaria* we can trace the disappearance of the centripetal xylem and its replacement by pith, whereas in the creeping axis of *Selaginella spinosa* the centrifugal xylem appears to have assumed the position usually occupied by the centripetal, or, in other words the protoxylem is absolutely central. Another objection to the view that the exarch condition is primitive lies in the fact that according to latest observations the hypocotyl of *Selaginella* always contains an endarch protostele (8). This is a serious objection to considering exarchy as primitive, for, in a general way, subject to many exceptions, the phylogeny of the stele is normally repeated in its ontogeny. But on comparative grounds there are very strong reasons for regarding exarchy as primitive. Not only was such a condition clearly the primitive one of the older dendroid Lycopods, but it is surely a very significant fact that *Miadesmia*, the only herbaceous Palæozoic Lycopod whose anatomy is known, possessed an exarch protostele (1).

Besides the exarch and endarch monostele there are various other types of stele. *S. Galeottii*, for example is bistelic (11); such bistely may well have arisen by the division of a single stele such as that of *S. spinosa*. *S. Braunii* may show an intermediate stage, for its creeping axis is at first monostelic, but becomes bistelic, while the erect stem remains monostelic, the two steles of the creeping axis uniting to form its stele. The majority of species of the genus are, however, monostelic, and their steles dorsiventral; this dorsiventrality of the stele is nearly always associated with heterophylly. The single stele of these forms is ribbon-shaped, and has one dorsal and two marginal strands of protoxylem; it is easy to see how this stele might be evolved from the exarch protostele *pari passu* with the assumption of a dorsiventral habit. In some tristelic species the dorsal protoxylem of the ribbon-shaped stele becomes a dorsal cord in the young plant and a dorsal stele in the mature plant, while the two marginal protoxylems also become separate. In other species, such as *S. inæqualifolia*, there are, besides these three

principal steles, other accessory ones (11). Mr. Tansley, in a recent course of lectures, suggested that the multiplication of the steles of *S. inæqualifolia* might be due to an increase of branching, for while the leaf-traces are still mainly given off from the original central cylinder, the accessory steles contribute to the formation of the branch traces. *S. laevigata* var. *Lyallii* has a dicyclic solenostelic rhizome and a highly polystelic erect stem. If we suppose (as seems reasonable from an analogy with the Ferns) that the internal strand of the rhizome arose, in the phylogeny, as a thickening of the edges of the gap in the woody ring, formed in this case by the departure of a branch-trace, and that this thickening became detached as an independent cord fusing at intervals with the outer stele, it is clear that there must have been among the ancestors of this species a form in which the rhizome possessed a single solenostele without an internal strand. It seems equally reasonable to suppose that this solenostele was derived from a protostele, for the evolution of solenostely from protostely, has often been traced, though not in this phylum, where indeed solenostely appears to be very rare. When traced upwards the outer ring-stele of the rhizome passes into the four principal leaf-trace-bearing steles of the erect stem; these therefore apparently represent the original hypothecated protostele; the numerous accessory steles are presumably of secondary origin.

Another point of considerable interest is that the base of the aerial stem of *Selaginella spinulosa* shows secondary growth in thickness (9). This character would seem to be best regarded as a recently acquired one, for it is not known in any other species and the genus as a whole does not appear to be reduced, since we found reason to conclude that there had been within the genus an evolution from a cylindrical protostele to a dorsiventral stele, to a dicyclic solenostele and to polystely. The genus thus appears to be on the up-grade of evolution and in *Selaginella spinulosa* the increasing complexity seems to have shown itself in the formation of a small amount of secondary xylem.

In the recent genus the fructifications are cones, but M. Halle has lately shown that in the Carboniferous *Selaginellites* (*Lycopodites*) *elongatus* the sporangia were borne in the axils of ordinary leaves, as they are in some species of *Lycopodium* (12). This may well be a primitive condition, but in that case heterospory must have preceded the evolution of a cone; if so the strobiloid condition has originated independently in *Lycopodium* and *Selaginella*. The fact

that the megasporangia of *Selaginellites elongatus* contain twenty to thirty spores gives some support to the view that this species, coming from the Middle Coal Measures (18), is relatively primitive. In the strobili of *Selaginella* the sporangia originate not from the sporophylls, but from their axils, or even from a group of cells belonging to the axis, situated distinctly above the sporophylls (5). In the fossil *Miadesmia* the sporangia are epiphyllous. This condition is probably primitive, for in all the known palæozoic Lycopods the sporangia seem to have been borne on the leaves. It was concluded in the first and second articles of this series that the sporangia of the Sphenophyllales and Equisetales were also primitively leaf-borne; and if, as seems likely, these two phyla had a common origin, though a very remote one, with the Lycopodiales we should expect the sporangia of the latter to be epiphyllous in the more primitive forms. Professor Bower, however, regards the epiphyllous or axial position of the sporangium as an overrated character (5).

Miss Lyon has shown that in *Selaginella rupestris* only one megaspore usually matures, though exceptionally there may be two (17). In most species there are four megaspores in a sporangium; a less advanced type of heterospory occurs in the Carboniferous *Selaginellites snissei* and *S. elongatus* where the megaspores seem to have been more numerous, there being sixteen to thirty in a single sporangium (12). Certain Coal Measure species, however, had, like the ordinary species of *Selaginella*, only four megaspores in each sporangium (12), (20). The reduction of the megaspores to a single one is clearly a later specialization and connected with it we find, both in *Miadesmia* and in *Selaginella rupestris*, a retention of the megaspore within the sporangium and the formation of a seed. Even before the discovery of its sporangia M. Bertrand recognized the probable affinity of *Miadesmia* to *Selaginella* (3). In its anatomy it resembles the more primitive species of *Selaginella*, but the seeds of both genera were, nevertheless, clearly homoplastic developments, for those of *Miadesmia* are morphologically far more highly developed, since they are provided with a velum arising from the proximal end and leaving a circular micropyle at the distal end. Nevertheless the earlier stages of germination do not appear to have taken place within the spore of *Miadesmia*, as they do in the comparatively little specialized seed of *Selaginella rupestris* (16).

As regards the embryology, Dr. Campbell and others have figured the development of the suspensor arising by the first division

of the fertilized ovum (10). Miss Lyon, however, found none in *Selaginella apus* (18); probably its absence there is a secondary character, for its absence is hitherto only recorded in that species, and a suspensor, though one of varying importance, is characteristic of *Lycopodium*, which, though not closely related to *Selaginella*, probably comes nearer to that genus than any other living form.

As regards the affinities of the Selaginellaceæ with the orders already discussed, they show many points of resemblance to the Lepidodendraceæ. There is a distinct resemblance between the general anatomy of the exarch protostele of the erect stem of *Selaginella spinosa* and a protostelic *Lepidodendron*. This probably does not indicate any direct connection between the two orders, for an exarch protostele is found in what are supposed to be the more primitive members of all the orders of the Lycopodiales. Other less important resemblances are the Stigmarian appendages, comparable to the monarch roots of *Selaginella*, and the secondary growth in thickness of *Selaginella spinulosa*. This secondary growth is, of course, a freshly acquired character not found in the other species; the mode of the secondary growth, moreover, is different from that of the Lepidodendraceæ and the analogy indicates no especially close affinity. The ligule, on the other hand, indicates a real, though not a very close, affinity. *Selaginella* appears to be a genus showing several modes of increase in complexity, but the complications all seem to be derivable from an exarch protostelic form. There is therefore no reason to suppose that the genus arose by reduction from the Lepidodendraceæ. Moreover we have evidence proving the existence of heterosporous herbaceous Palæozoic Lycopods and it is therefore very probable, as maintained by Dr. Scott, that *Selaginella* was derived from such herbaceous forms (20). In any case of the seeds of *Miadesmia*, *Selaginella* and *Lepidocarpon* each forms a culminating point of a distinct evolutionary series: that these genera never had a common seed-bearing ancestor is clear from the totally different structure of their seeds.

The relationship of *Selaginella* to *Isoëtes* is neither close nor clear; the absence of a strobilus or a suspensor in the latter, its relatively large leaves and epiphyllous sporangia, are all in striking contrast to *Selaginella*. The last character, however, is also found in *Miadesmia*, a genus that probably belongs to the Selaginellaceous cycle of affinity. As it is one of the oldest known members of that cycle it may well have been primitive in that respect. As pointed out in considering the affinities of *Isoëtes* to the Lepidodendraceæ

the absence of a strobilus in the former may, or may not, be primitive. But the most important difference between the Selaginellaceæ and the Isoëtaceæ is that the former have biciliate and the latter multiciliate spermatozoids. As biciliate spermatozoids are only known in *Selaginella* and the Lycopodiaceæ among Pteridophyta, there is a general presumption that the multiciliate ones of *Isoëtes*, though exceptional in the phylum, are the more primitive; but the relative primitiveness of the multiciliate type of spermatozoid will be best discussed later in considering the affinities of the phyla. The secondary growth in thickness of *Selaginella spinulosa* offers a mere analogy with that found in *Isoëtes*, for the details of the mode of growth are different. Heterospory may also have arisen independently in the two orders. It does, however, seem *possible* that the monarchy of certain roots of *Selaginella* may be a primitive character retained from a very distant ancestor, common to it, *Isoëtes* and the Lepidodendraceæ. The reasons for this are that it is a very rare condition among recent plants, but one prevalent among the Palæozoic Lycopods, and that there is no reason to believe that *Selaginella* has undergone any reduction, as all available evidence tends to prove that the genus is on the upgrade of evolution.

The order of the Lycopodiaceæ contains but two genera, *Lycopodium* and *Phylloglossum*. In considering their structure, the first vexed question that arises is: Is the protocorm primitive and its absence in the larger number of species of *Lycopodium* due to their reduction, or is it a later development of the embryo of *Phylloglossum* and of some species of *Lycopodium*? This so-called protocorm is a tuber, which appears in *Phylloglossum* to replace the true stems, and from which, in *Lycopodium*, the true stem arises later. Professor Bower at one time considered the protocorm a primitive organ (5); but he has since abandoned that view and now regards the presence of a protocorm as a recently acquired character and does not regard the protocorm as being the precursor of the leafy stem of the Pteridophyta. In his latest publication he maintains that the embryo Lycopod seems prone to parenchymatous swellings and that the foot and protocorm are of this nature. He continues: "A genus which shows two types of parenchymatous swellings in two distinct types of embryo, while both are absent from other species of the genus, cannot be expected to have ever had one of these as a constant feature in its ancestry. This consideration makes me doubt any general application of the theory of the "proto-

corm" even in the genus *Lycopodium*. These parenchymatous swellings may be looked upon as opportunist growths, rather than as persistent relics constant from a remote ancestry. This view is greatly strengthened by the occurrence of protocorm-like developments in isolated cases among the Angiosperms. *Phylloglossum* with its large storage "protocorm" would then be the extreme type of a line of embryological specialization, not a form preserving the primitive embryological characters of the whole race" (7). The opposite view, first elaborated by Dr. Treub and formerly held by Professor Bower himself (5), is held by Dr. Lang (15), by Professor Thomas (22), and by Miss Sykes (21). Dr. Lang brings forward several considerations in support of the primitiveness of the protocorm. He points out that the type of prothallus found in *Lycopodium cernuum*, *L. inundatum* and *L. salakense* is probably relatively primitive, since it is not modified in connection with epiphytism and with saprophytism. The habit of the gametophyte can legitimately be held to influence the extra-prothallial protocorm, for Professor Thomas has shown that, at least in *Phylloglossum*, the latter organ is formed directly the young sporophyte escapes from the embryo, while the prothallus often retains its vitality for some time afterwards. If, then, we admit that the prothallus of these species of *Lycopodium* is relatively primitive (and this seems to be the case as will be shown later), and that the structure and habit of the gametophyte may affect the young sporophyte, we should expect the young conditions of *L. cernuum*, *L. inundatum*, and *L. salakense* to be relatively primitive. Now these three species and *Phylloglossum* (whose prothallus corresponds in essentials to theirs (22)) are those that develop a protocorm. Moreover, as Dr. Lang points out, the young sporophytes growing from the root tubercles of *L. cernuum* also produce protocorms (15). These can hardly be regarded as embryological specializations. It seems, too, that the occurrence of a protocorm in species of both genera supports the primitive nature of this organ, for it would be natural to suppose that their common ancestor possessed a protocorm. But it is clear that *Phylloglossum* is very close to *Lycopodium*, and it has been suggested (2), (21) that it arose by reduction from the section of the genus *Lycopodium* that includes *L. cernuum*, and that it should not be separated from *Lycopodium*. In support of the primitiveness of the protocorm Dr. Lang alludes to the presence of a rudimentary protocorm bearing rhizoids in an example of *L. Phlegmaria* (15). Professor Bower objects that the position

of the root on the swelling seen in this specimen of *L. Phlegmaria* does not correspond to the position of a root on a true protocorm (6). But even if this swelling were a true protocorm it would not prove the primitiveness of the latter, though it would weigh on that side of the question. Again, if the protocorm were primitive, we should expect that it would be at least equally well developed in the Palæozoic and Mesozoic ancestors of the Lycopodiaceæ as in *Phylloglossum*, where it is quite bulky enough to be fossilized. No trace of a protocorm has been found in connection or associated with Palæozoic or Mesozoic *Lycopodites*. But a stronger argument against the primitiveness of the protocorm is that if we regard it as the forerunner of the leafy stem we cannot avoid supposing that it was found in the common ancestor of the phylum, unless we make the unwarrantable assumption that the stem of *Lycopodium*, the anatomy and histology of which are essentially similar to those of other primitive Lycopodiales, had a different origin from the stem of other Lycopods. But the protocorm only occurs in the Lycopodiaceæ, where it is associated with late and comparatively small development of the vascular tissues. It is very difficult to imagine that certain Lycopodiaceæ have retained up to the present day an organ, the forerunner of the leafy stem, which had in certain members of the phylum, in the Lepidodendraceæ, been replaced by stems that had already attained dendroid proportions in the Devonian age. Another of Professor Bower's arguments against the primitiveness of the protocorm rests on the want of sharp differentiation between the protophylls or leaves borne by the protocorm and the ordinary vegetative leaves. He says that even in *Phylloglossum*, where the distinction between the two is usually more marked, intermediate forms between protophyll and sporophyll have been seen (6). The latter part of this statement is in direct contradiction to an observation of Professor Thomas, who denies the existence, in his specimens, of transitions between sporophylls and protophylls (22). It is fair to add that in a former paper Professor Bower laid great stress on the absence of forms truly intermediate between sporophylls and protophylls in *Phylloglossum* (5). But even if we accept Professor Thomas' statement of the sharp differentiation between protophylls and sporophylls of *Phylloglossum* we must admit that in *Lycopodium ceruuum* the protophylls merge gradually into the foliage leaves. The absence or feeble indication of any transition from the protophylls to the other appendages in *Phylloglossum* would agree with Professor Bower's suggestion that this genus, with its large protocorm, may well be the extreme type of a specialized line.

In discussing the phylogeny of the protocorm too little attention has been paid to the anatomy of *Phylloglossum*, though M. Bertrand published an excellent account of it as long ago as 1885 (3). Dr. Campbell, in the last edition of his "Mosses and Ferns" states that the anatomy of the vegetative organs, examined by Bertrand, corresponds closely to that of *Lycopodium*, but that the tissues are simpler (10). Professor Bower in his recent "Origin of a Land Flora" discusses the nature of the protocorm, but makes no mention of the peculiarity of the vascular tissue of *Phylloglossum*, though the structure of the stele has an important bearing on the primitiveness of the genus and therefore of the protocorm (7).

The protocorm or tuber of *Phylloglossum*, which appears to replace the stem, bears protophylls and roots, and in exceptionally vigorous plants its apex grows out into an axis terminated by a cone. According to M. Bertrand's account the lower part of the protocorm contains no vascular tissue; vascular tissue is first developed just above the insertion of roots and just below the insertion of the leaves; it consists of an anterior and a posterior mass of xylem embedded in phloem. The peduncle of the strobilus also shows, throughout most of its course, internal and external phloem; here, in typical cases, we have the type of structure which has since been called solenostelic. The structure of the peduncle varies considerably, and, in places, the xylem forms a solid protostelic mass, or the centre of the xylem may be occupied by a few phloem elements. The pedicel, arising from the protocorm and bearing the tuber of the next year's growth, is also, in parts, provided with internal phloem; it is probably best regarded as a modified cauline portion. What is important for the present discussion is that the presence of internal phloem in several parts of *Phylloglossum* renders it almost impossible to regard the vascular tissues of the latter as equally primitive with the protostelic species of *Lycopodium*, *Selaginella* or *Lepidodendron*. Internal phloem is not found in any of the more primitive Lycopodiales; indeed, outside *Phylloglossum* it is so far only known in *Selaginella laevigata*, var *Lyallii*, where, as shown above, it is probably a recent modification. On the other hand it does not seem conceivable that so small a plant as *Phylloglossum* should have acquired internal phloem; therefore it would seem that this genus owes its present simplicity to reduction rather than to the retention of primitive characters. But on this view it is surprising that no traces of internal phloem have been found in the protocorm-bearing species of *Lycopodium*, to which *Phyllo-*

glossum is clearly related, and from which it has been suggested that it arose by reduction. As the protocorm of *Phylloglossum* is the largest and longest lived of the order, it would be possible to consider that it had recently acquired internal phloem, but this would not account for the internal phloem of the axis of the cone and the pedicel of the young tuber. In these the internal phloem can hardly be other than a vestigial character, retained in spite of reduction.

On the whole then, although the evidence is somewhat contradictory, the probability is that the possession of a protocorm is not a primitive character of the Lycopodiaceæ. It is almost certainly not primitive for the Lycopodiales as a whole.

Turning to the general anatomy we find that *Phylloglossum* differs from *Lycopodium* in two points [besides the occasional presence of internal phloem already considered. In *Phylloglossum* the xylem of the protocorm and of the axis of the cone is mesarch, while in *Lycopodium* it is exarch. Since we have seen that exarchy is characteristic of what appear to be the more primitive members of all the Lycopodial orders, the natural conclusion is that the mesarchy of *Phylloglossum* is less primitive than the exarchy of *Lycopodium*. On the other hand it seems very unlikely that a plant so small, and possessing so little vascular tissue as *Phylloglossum* should have acquired fresh and centrifugal xylem. This points, as did the presence of internal phloem, to the hypothesis that *Phylloglossum* is reduced from a form less primitive, in this respect than *Lycopodium*. This is, of course, incompatible with the suggestion mentioned above, that *Phylloglossum* arose by reduction from a section of the genus *Lycopodium*.

The second difference is that the traces of the protophylls are, sometimes at least, quite free from the vascular strand running from the protocorm to the axis of the strobilus and are attached to the root-traces. This peculiarity seems to be unique, and is presumably a recently acquired character (one possibly correlated with reduction of the stem), for ancestral characters tend to reappear in allied forms.

Mr. Jones has recently shown that two principal types prevail in the anatomy of the mature stem of *Lycopodium*, but that the young plant in all cases contains a single triarch or tetrarch, solid, exarch stele. In the course of development the protoxylem groups increase in number by the splitting and shifting of the strands. The phloem either differentiates in bands, or in isolated patches breaking up

the xylem. Of these two types the banded one is on the whole characteristic of creeping stems, and the other of tropical forms. It should be added that, according to Mr. Jones' researches, the protoxylems of the banded types of stele continue to increase by fission, while, in some cases, branches show a reduction to the tetrarch type of the young stem. Mr. Jones considers that these two types represent two lines along which the development of the vascular structure of the genus has proceeded (14). He does not seem to contemplate the derivation of one from the other. It seems clear that the banded type of stele, was, in the phylogeny, evolved from an exarch protostele, with projecting angles like those found in the young stem. These protoxylems seem at first to have been three or four, and with their increase in number the phloem seems to have increased also, and to have broken up the xylem. *L. selago* seems to have retained a rather primitive condition, the protoxylems being few, not more than seven, and the phloem not having split up the xylem completely, as the latter still forms a solid mass in the centre of the stem. *Lycopodium tetragonum* may be even more primitive, for there are only four protoxylems, but this species was only cursorily examined by Mr. Jones. Of *Lycopodium alpinum*, Mr. Jones says "there is a great tendency to form phloem patches or phloem islands; and in other respects, notably the irregular differentiation of the xylem near the apex, it forms a connecting link with the second group of Lycopods, . . . which is characterized by the separation of distinct phloem islands" (14). Mr. Jones notes a similar tendency in *L. serratum*. These facts seem to the present writer to indicate that the type of stem in which phloem and xylem are intermingled arises by the greater development of the xylem in a banded form, until the wood, spreading in most directions, come to surround the phloem. Indeed it is difficult to see otherwise how the patches of phloem came to be enclosed by xylem. The irregularity of these phloem islands show that they do not correspond to the "internal phloem" found in solenostelic Ferns and recorded by M. Bertrand in *Phylloglossum*. Mr. Jones merely states that "the phloem differentiates as isolated groups which break up the continuity of the xylem" (14). This is no doubt a very good description of the ontogenetic process, but it does not explain the phylogeny satisfactorily.

The fructifications are always homosporous; they may be definite strobili, as in some species of *Lycopodium* and in *Phylloglossum*, or the fertile and sterile leaves may be essentially similar

and form alternating zones, or finally in *L. compactum* and *L. Trencilla* all the leaves of the mature plant appear to bear sporangia (6), (7). It is generally conceded that the forms without definite cones are the more primitive, whether on account of the absence of differentiation of the sporophylls from the sterile leaves or of the sterile leaves from the sporophylls. Professor Bower, being a strenuous supporter of the antithetic origin of the sporophyte, holds that the vegetative leaves are sterilized sporophylls and that the most primitive type is therefore that of *L. compactum*, where every leaf, or at least every leaf persisting on the mature sporophyte bears a sporangium. The question of the the antithetic or homologous origin of the sporophyte cannot be considered here, but the enormous age of the vascular sporophyte and the presence of Lycopods with a large vegetative system in the Devonian, or perhaps even in the Silurian, renders it unlikely that *L. compactum* and *L. Trencilla* should have retained to the present day the hypothetically primitive condition of a sporophyte fertile throughout. Other species all have sterile basal regions, sometimes of considerable length. In the present condition of our knowledge, neither the homologous nor the antithetic origin of the sporophyte can be regarded as proved, or even probable. In view of the fact that all known Palæozoic forms of Lycopods were provided with sterile leaves (except *Spencerites*, the cone of which alone is known, bearing small bracts below the region of the sporophylls), and that in many of them the vegetative system attained to tree-like proportions, it would seem more natural to regard the complete fertility of the sporophyte of certain species of *Lycopodium* as probably secondary, and possibly due to the reduction of the vegetative part of the plant. The Lycopodiaceæ are certainly very primitive plants, for since the removal of the Psilotaceæ from this phylum they constitute the only homosporous order. Perhaps, therefore, the want of differentiation between leaves and sporophylls and the non-strobiloid condition of certain species of *Lycopodium* may be primitive characters. In *Lycopodites Stockii* the sporangia were borne on sporophylls, aggregated into cones, but these were not sharply defined below and some of the leaves below the cone bore sporangia (7). The discovery of a tree-like Lycopod without a definite strobilus (*Pinakodendron*), and of a non-strobiloid herbaceous plant apparently very close to *Selaginella* (*Selaginellites elongatus*) (12), renders it not improbable that the earliest members of the Lycopodiales began to diverge from the

contemporary representatives of other phyla before acquiring a definite strobilus.

The gametophyte of *Lycopodium* has been the subject of careful comparative study by Dr. Lang (15). In the *Lycopodium cernuum* type of prothallus, which is characteristic in all essentials of *L. inundatum* and *L. salakense*, and of *Phylloglossum*, there is a primary tubercle bearing one or two more or less filamentous outgrowths, that later become thickened so as to be externally indistinguishable from the tubercle. The latter is almost always occupied by an endophytic fungus, and the upper part of the prothallus contains chlorophyll. In *L. cernuum* and *L. inundatum* the prothallus is crowned by leaf-like lobes absent from *L. salakense* (15) and *Phylloglossum* (22). Dr. Lang points out that the prothallus of *L. selago* often shows a distinct resemblance to this type. Normally it is subterranean and a more or less cylindrical body devoid of chlorophyll, but when exposed artificially or naturally to light it develops a considerable amount of chlorophyll (15). This at once suggests a comparatively recent origin for the subterranean prothallia from a form such as that found in *L. cernuum*. This prothallus appears to be more or less independent, though the endophytic fungus associated with it may indicate a partially symbiotic habit. No primary tubercle is found in *L. selago*, but the germination of its prothallus has not been observed and in later stages the primary tubercle is often unrecognizable. The leafy lobes are not of course found in this subterranean form, but these are absent in *L. salakense* which is distinctly of the *L. cernuum*-type. Dr. Lang writes: "Besides this form of prothallus, the resemblance of which to the *L. cernuum*-type will be evident, elongated cylindrical forms which originate by growth becoming localized in one portion of the meristematic zone are found. The interest of these will be seen in connection with the *L. Phlegmaria*-type of prothallus" (15). Dr. Lang's conclusion that the *L. selago*-type of prothallus, found also in *L. complanatum* and *L. alpinum*, originated from the *L. cernuum*-type by adaptation to a subterranean habit seems justified. The prothalli of *L. annotinum* and *L. clavatum* are not unlike the prothallus of *L. selago*, but the meristem gives rise to an expanded, more or less irregularly lobed, portion, much larger than the conical body to which it is attached. These species develop chlorophyll. The other species of *Lycopodium* in which the gametophyte is known are all of them tropical and the prothallus is a highly branched structure. This form of prothallus is known as

the type of *L. Phlegmaria*. Concerning it Dr. Lang writes: "This form suggests comparison with the modification of the prothallus of *L. selago* referred to above, which was seen to arise by the localization of growth in one part of the meristematic zone" (15). Further on Dr. Lang sums up the inter-relationships of the prothalli very lucidly in the following words:—"The similarity in ground plan of the prothalli would appear rather to indicate that they are all more or less profound modifications of a type not unlike that of *L. cernuum*. The two forms of prothallus found in *L. selago* give the clue to the more specialized saprophytic types, which, in the deeper growing subterranean species, retain the radial symmetry while becoming modified in shape. On the other hand the type of prothallus growing in rotting wood (that of *L. Phlegmaria*) has lost the radial symmetry and consists of cylindrical but more or less clearly dorsiventral branches. The variability of several characters, such as the presence or absence of leaf-lobes, the distinctness of the primary tubercle, and the passage from radial to dorsiventral symmetry within the limits of the *L. cernuum*-type, when taken in conjunction with the variety of form of the *L. selago* prothallus appears to justify such a view as that suggested above" (15). Professor Thomas' discovery, since the above was written, of the prothallus of *Phylloglossum* (22) strengthens Dr. Lang's view of the primitiveness of the *L. cernuum*-type of prothallus, for the reappearance of a character in an allied genus increases the probability of that character being primitive.

The affinities of the Lycopodiaceæ with the other orders of the phylum do not appear to be close. From the Lepidodendraceæ they differ in the absence of a ligule and of secondary growth in thickness, in their constant homosporous, and in the fact that their fructifications are not always definitely strobiloid, as are those of the Lepidodendraceæ (except perhaps *Pinakodendron*). Mr. Jones (14) and Mr. Hill (13) have, however, found in the sporophylls and leaves of some species of *Lycopodium*, mucilage-canals, which the latter writer compares to parichnos. Owing to the small size of the leaves of *Lycopodium*, these parichnos are presumably an ancestral character, inherited from a larger leaved form. Miss Sykes points out "... that it is possible to regard *Spencerites* as an ancient connecting link between the old Lepidodendra and the Lycopodiums, perhaps one of the first of a chain of genera which were to form a long reduction series" (21).

Very striking similarities between *L. cernuum* and *Spencerites*

have quite recently been brought to light by Dr. Lang. He has shown that the peltate form of the mature sporophyll of *L. cernuum* is due to the disappearance of a mass of mucilage from the base of the bulky sporophyll, and suggests that the pseudo-peltate form of the sporophyll of *Spencerites* is also due to the fact that a similar mucilaginous mass has escaped fossilization. This suggestion is borne out by other points of close similarity between the sporophylls of the two genera. In *L. cernuum* the lower surface of the sporophyll bears a small projection; a similar projection occurs on the "dorsal lobe" of the sporophyll of *Spencerites*, the dorsal lobe on this view representing the base of the sporophyll, the more adaxial portion of which has been secondarily hollowed out by the disappearance of a mass of mucilage (16). Dr. Lang further points out that in the young condition the sporophyll base of *L. cernuum* is coherent laterally with the bases of the sporophylls (belonging to the next whorl) on each side of it, and that though recent investigators have not referred to any sign of cohesion between the sporophylls of *Spencerites*, indications of such a condition were reported by Williamson in his description of the genus (16). The similarities pointed out by Miss Sykes and Dr. Lang between the cone of *Spencerites* and that of certain species of *Lycopodium* are interesting, in view of the fact that, so far as we know, *Spencerites* was homosporous, though so few specimens are known that the presumption of homospory is but weak. Among the most interesting results of Miss Sykes' researches is the discovery of lignified cells in the sporangial pedicel of *Phylloglossum* and of the larger species of *Lycopodium*; these, though forcibly recalling vascular tissue, and though very close to the sporophyll-trace, are never connected with it, though in one case they were in connection with the lignified cells surrounding the trace. Miss Sykes, in a footnote, asserts the presence of such cells in Miss Berridge's preparation of *Spencerites* (21); but both the latter and Dr. Scott assert the complete absence of vascular tissues in the projection of the sporophyll bearing the sporangium of *Spencerites* (2), (20). But though Miss Sykes and Dr. Lang's suggestion of a possible connection between *Spencerites* and *Lycopodium* is very valuable, it is difficult to agree with the former in her attempt to connect the former genus with the typical ligulate *Lepidodendraceæ*. She suggests that the small lump of tissue found between the sporangium and the distal end of the sporophyll of *Spencerites* recalls the ligule of *Lepidodendron* (21). But the ligule is situated beyond the insertion

of the sporangium, while the projection is at the insertion and bears the sporangium. Miss Sykes suggests that the absence of a ligule in *Spencerites* and *Lycopodium* may be due to the fact that the sporangia of these genera are sufficiently protected by the sporophyll from too great evaporation and that the mucilage, once secreted by the ligule, is no longer necessary (20). This hardly seems a sufficient reason to account for the absence of a ligule, which appears to be a very persistent organ, constantly present in the ligulate cycle of affinity. The sporangia of *Lepidocarpon* and of those species of *Isoetes* that possess a velum appear to be more protected than the sporangia of the Lycopodiaceæ; yet their ligules show no indications of reduction. Thus even if, as seems probable, the Lycopodiaceæ are descended from *Spencerites* or allied forms there is at present little to connect that genus with the Lepidodendraceæ, though the discovery of its vegetative organs may bring it nearer to them.

The Lycopodiaceæ show perhaps even less indication of affinity to the Isoëtaceæ; this is what we should expect if the latter order is reduced from the Lepidodendraceæ. *Isoetes* approaches the Lycopodiaceæ in point of size, and resembles certain species of *Lycopodium* in being non-strobiloid. But this condition may well be secondary in a form clearly so reduced as *Isoetes*, while the absence of a ligule and of secondary growth in *Lycopodium* and its biciliate spermatozoids are important differences between the two genera.

The Selaginellaceæ are perhaps the order of the phylum coming nearest to the Lycopodiaceæ, though even they are very remote from the latter. The anatomical evolution of the stem has evidently run a completely independent course from the time when the exarch protostele, characteristic of the primitive members of every order of the phylum, was laid down. The ligule and the heterospory even of the Palæozoic Selaginellaceæ mark out the two orders as having been distinct from a very early period; but the general habit, the absence of secondary growth in the members of both orders (except *Selaginella spinulosa*), the apparently constant production of a suspensor (except in *Selaginella apus*), and, above all, the biciliate spermatozoids, may be indications of a real, though very distant, relationship between the two orders. Though it is difficult to distinguish certainly between impressions of *Selaginellites* and *Lycopodites* it is probable that forms similar to the Lycopodiaceæ and referable to the latter genus existed even in the Palæozoic age. This may explain the isolation of existing Lycopodiaceæ.

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TYLOSES IN TRACHEIDS OF CONIFERS.¹

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[WITH PLATE V.]

TYLOSES have generally been considered to be absent from the wood of gymnosperms. Molisch² examined seven hundred species of vascular plants in order to determine the distribution of these peculiar growths, and came to the conclusion that they are altogether lacking in vascular cryptogams and gymnosperms. But he was shortly followed by Raatz,³ who described tyloses occurring as the result of wounding in the stem and root wood of *Pinus* and several other genera. Raatz's paper has apparently been overlooked, for in so recent a paper as that by Weiss⁴ is the following statement, "Their mode of origin, too, upon which Molisch insists, as ingrowths from surrounding parenchymatous cells, seems to preclude their formation in gymnosperms where wood parenchyma is generally absent." Concerning this statement it should be pointed out that absence of wood parenchyma by no means precludes the formation of tyloses, for as Raatz figures, and the following account shows, tyloses in coniferous wood arise from the parenchymatous cells of the medullary rays. Up to the present our knowledge of the distribution of these structures may accordingly be summed up thus: tyloses occur in a large number of angiosperms as intrusions into vessels, and in gymnosperms (1) in the resin canals of a few genera, especially *Pinus*, and (2) in the tracheids of a few genera but exclusively as the result of wounding. To this should be added the observations of Conwentz that tyloses occupy the cavity of vessels in *Cyathea*, and that of Williamson⁵ and of Weiss (l.c.) who find them in the fossil fern *Rachiopteris*.

The observation of certain protrusions from the medullary ray cells into the tracheids in the heart wood of the root of *Pinus*

¹ Contributions from the Phanerogamic Laboratories of Harvard University, No. 12.

² Molisch, H. Zur Kenntniss der Thyllen. Sitzungsber. d. K. Akad. d. Wiss. zu Wien 97; 7; 1888.

³ Raatz, Wm. Ueber Thyllenbildung in den Tracheiden der Coniferenhölzer. Berichte d. deutschen Bot. Ges. X., pp. 183—191. pl. 10. 1892.

⁴ Weiss, F. E. On the Tyloses of *Rachiopteris corrugata*. NEW PHYT., V., pp. 82—85. 1906.

⁵ Williamson, W. C. Organisation of the Fossil Plants of the Coal Measures. Part VIII. Phil. Trans., 1877, Part X. Phil. Trans., 1880.

strobis has led me to reinvestigate the subject, for the root in question bore no evidence of wounding. I have studied the root-wood of as many gymnosperms as were available, and have extended the observations to other parts such as wounded branches, the cone axis and the short shoots. For valuable aid in securing material I am indebted to the following: Mr. C. G. Fraser, Professor T. C. Frye, Mr. Andrew Jeffrey, Professor G. R. Lyman, Mr. J. Murdoch, Mr. R. Thomson, the Government of British Columbia, and especially to Professor G. L. Goodale and Mr. R. Cameron of the Harvard Botanic Garden.

The typical appearance of the structures in question is shown in a tangential section through the heart wood of the root of *Pinus austriaca* (Pl. V., Fig. 1). The section was stained in Haidenhain's hæmatoxylin followed by safranin, and this fact accounts for the dark colour of the tyloses, which is due not so much to the cell contents as to the nature of the wall, as will be explained later. The general form of the tylosis is that of a more or less elongated vesicle protruding from a pit in the wall of a central cell of a medullary ray into an adjoining tracheid. The appearance is in fact precisely similar to what may be observed in the narrower vessels in a wood such as hickory; in both cases the tylosis fills the whole width of the vessel or tracheid on account of their small diameter. The origin of the tylosis is clearly shown in at least one case in this figure, and appears even more clearly in certain of the other figures. From one of the "Eiporen" of a central medullary ray cell the thin membrane protrudes, extending farther and farther into the lumen of a tracheid. Naturally the marginal cells of the rays do not give rise to tyloses, for they have lost their protoplasmic contents and have assumed the office of tracheids. A number of marginal cells destitute of tyloses may be seen in the various figures. A marginal cell may however contain a tylosis, which has entered through a pit on the wall between a marginal and a central cell; apparently this is not of frequent occurrence. Early stages in the formation of tyloses may be seen in Fig. 2, which is a more magnified photograph of a section similar to that represented in Fig. 1, *viz.*, from the heart wood of the root of *Pinus austriaca*. Near the upper end of the ray is a cell in which the membrane of a pit on each side of the cell is inflated, and just below this is a slightly older tylosis. The protoplasmic membrane of several of the other cells have shrunk, but it will be noticed that the lowest cell (a marginal cell) is unaffected. Appearances similar to this but less pronounced

have been figured by Penhallow¹ for the stem wood of *P. reflexa*. It would be interesting to ascertain whether the wood of other parts of the tree in this species shows well-marked tyloses.

Although these structures are best shown in a tangential section, they may be seen in transverse section also, as is represented in figures 3 and 4. In either case they are rendered much more easily visible by the application of a hæmatoxylin stain (especially Ehrlich's), and may in fact easily be overlooked in an unstained preparation, on account of the delicacy of their walls and because they fit so tightly against the walls of the tracheid. Fig. 3 shows early stages in the formation of tyloses as are commonly exhibited in sections through the heart wood of roots of *P. strobus*. The figure shows both central and marginal cells of two medullary rays, and the protrusions from the pits of the former sort. In one corner is visible part of a resin canal with its usual complement of tyloses. Apparently in this species the tyloses do not attain the development shown in several other species, for in material collected in localities as far apart as Cambridge, Mass. and near Georgian Bay, Ontario, no well-developed cases were found. Near the pith of roots of *P. strobus* the outgrowths are frequently exceedingly numerous, but are not confined to this region, for they extend throughout the heart wood, becoming scarce as the sap wood is approached. They may occur in any part of an annual ring, and are not more numerous in spring wood than in summer wood.

Further stages in the growth of a tylosis are shown in Figs. 5 and 6. The tylosis increases in length until in some instances it extends to the end of a tracheid, as may be seen in Fig. 6, which is from a tangential section through the first year's growth of a cone of *P. ayacahuite*. The tylosis in question has also extended into an adjoining tracheid by way of one of the pits. The same tylosis illustrates, though not very clearly, another stage of growth, namely the appearance of a cross wall. Evident instances of cross walls have been observed in other species, for example, *P. rigida*, but this stage does not seem to occur by any means as frequently as in the tyloses found in the vessels of dicotyledonous woods. Fig. 5 illustrates in a diagrammatic way the appearance and origin of the abundant tyloses in the root of *P. palustris*. What may be regarded as the final stage in growth is the more or less extensive filling of a tylosis with a resinous material. This is illustrated by the photograph of a transverse section through the cone axis of

¹ Penhallow, D. P. A manual of the North American gymnosperms. Boston, 1907.

P. palustris (Fig. 4), in which the tyloses are usually completely filled with a dark coloured material. Appearances such as this need not be confounded with deposits of resin in tracheids, for the shape of a tylosis in tangential section is distinctive, having rounded ends, while the masses of resin in the tracheids of *Dammara* are in the form of double concave lenses.

As to the extent of occurrence of tyloses, it may be gathered from the preceding paragraphs that there are two regions of the plant in which they may be found, (i.) in the heart wood of the root, (ii.) in the first year's growth of the cone axis. It should now be added that, so far as my observations go, they are confined to the genus *Pinus*. I have examined the root wood of thirty-two species of gymnosperms, belonging to thirteen genera including *Pinus*, *Picea*, *Larix*, *Pseudotsuga*, *Abies*, *Tsuga*, *Taxodium*, *Juniperus*, *Thuja*, *Taxus*, *Araucaria*, *Agathis*, *Ginkgo*, also the cone axes of twenty-three species belonging to eight genera, namely *Pinus*, *Picea*, *Pseudotsuga*, *Cedrus*, *Abies*, *Tsuga*, *Araucaria*, *Agathis*. The material has come from a great variety of habitats, and in some cases the root wood has included wounded specimens. Only a few observations on stem wood have been made in connection with this study, but the large number of sections of coniferous wood passing through my hands in class-work have failed to furnish any instances of tyloses in stems of gymnosperms. These results are at variance with those of Raatz (l.c.), who states that tyloses occur in *Picea excelsa*, *Larix europæa*, *Abies pectinata*, *Thuja occidentalis*, as well as *Pinus excelsa*, *P. silvestris* and *P. strobus*. Unfortunately the only figures in Raatz's paper are of species of *Pinus*. It may at least be suggested that deposits of resin which are common in wounded root wood may have been mistaken for true tyloses. My observations indicate that that these growths occur in both sections of the genus *Pinus*, namely *P. strobus* (in root and cone), *P. monticola* (root), *P. ayacahuite* (cone) among the soft pines, and *P. palustris* (in root and cone), *P. rigida*, *P. austriaca*, *P. contorta*, *P. resinosa* (root), *P. silvestris* (cone) among the hard pines.

Wounding has so frequently been adduced as the cause of tyloses that I have given special attention to this phase of the problem. The presence of wounds may be indicated by distortion of the tissues, by resin in the tracheids, and in such genera as *Abies* and *Sequoia* by the production of a ring of resin canals. Judged by these criteria some of the specimens examined were wounded, while others showed no signs of abrasion. In some

of the species examined both wounded and healthy specimens were available. Outside the genus *Pinus*, wounded and perfect specimens alike showed no tyloses. Within this genus, wounded roots appeared to have the tyloses somewhat better developed than did perfect roots.

In order to investigate further the effect of wounding, two series of experiments were made. In the first of these, stout galvanized iron wire was tightly bound in the form of a ligature around roots of the following species: *Pinus strobus*, *P. austriaca*, *P. resinosa*, *Picea excelsa*, *Larix occidentalis*, *Abies subalpina*. These trees were growing in the Harvard Botanic Garden. After remaining ligatured for two months (June to August, 1907), the sections of the various roots were removed from the trees, preserved and later examined. In the case of *P. strobus* the last annual ring showed only slight inflations of the medullary ray cells. It will be recalled that the heart wood of this species ordinarily does not show well-developed tyloses. Sections of *P. austriaca* and *resinosa* showed a few unquestionable tyloses in the last annual ring; these roots were too young to have heart wood. The roots of *Picea* and *Larix* showed areas of distorted elements, including both parenchyma and tracheids, but no tyloses, while *Abies* responded to the treatment by the usual production¹ of a large number of traumatic resin ducts, but no appearance of tyloses.

The second series of experiments consisted in cutting off branches and setting the cut ends in vessels containing water. The species thus treated were *Pinus strobus*, *P. flexilis*, *P. austriaca*, *P. resinosa*, *P. silvestris*, *Larix occidentalis*. The branches were left with the cut ends in water for two months, then preserved and examined. In no case were any tyloses observed. It was long ago observed by Unger² that shoots of *Canna* treated thus showed an abundant development of tyloses near the cut end, and upon these grounds he concluded that tyloses are produced as the result of wounding.

These experiments acquire additional interest when considered in connection with recent observations by Jeffrey. This author shows that resin canals are produced as the result of wounding in genera in which they are normally absent, *e.g.*, *Abies* (l.c.) and

¹ See Jeffrey, E. C. The Comparative Anatomy and Phylogeny of the Coniferales, Part 2. The Abietineæ. Mem. Boston Soc. of Nat. Hist. 6; 1., pp. 1—37. Pls. 1—7, 1905.

² Unger. Ueber d. Ausfüllung alternder u. verletzter Spiralgefässe durch Zellgewebe. Sitzungsber. d. Wiener Acad. 56, 1867.

Sequoia,¹ and he considers this phenomenon a reversion to the ancestral condition in which resin canals are normally present, as in the group *Pineæ*. There seems good reason for considering resin canals to be a feature of phylogenetic importance; are tyloses to be so regarded? According to the observations recorded in this paper, tyloses occur only in *Pinus*, which appears from the researches of Jeffrey and others to be a very old genus, but this does not necessarily imply that tyloses are a primitive feature. It is of interest to note in this connection that Conwentz² has reported the occurrence of tylosis-like growths in the tracheids of the amber producing conifers of the late Eocene, which were pines, though his observations have been called in question by Raatz. Moreover, tyloses have recently been described by Weiss (l.c.) as occurring in the tracheids of a fossil fern *Rachiopteris*, from the coal measures, so that they may fairly be regarded as an ancient structure. The occurrence of tyloses in the cone axis seems to be a significant fact, for the reproductive axis is a region where ancestral features are prone to persist. It may also be remarked that roots have a more primitive structure than stems, and it is in the roots that tyloses are most abundant, at least in the conifers. But the failure to produce these growths by means of wounding in other genera than *Pinus* does not argue in favour of their being ancestral structures. Perhaps the production of tyloses is to be explained on purely physiological grounds, as is indicated by the experiments on wounded roots. But it is still unexplained why tyloses frequently occur in roots and seldom in stems of pines. Raatz's suggestion that roots are more subject to injury by tramping, etc., fails to account for the prevalence of tyloses in heart wood. It is well known that in the genus *Pinus* it is only in the heart wood that tyloses fill the resin canals, and it may be argued that production of these growths in both resin canals and tracheids is involved in the transformation of sap wood into heart wood, and that in both cases the tyloses serve to check the entrance and progress of fungal hyphæ. It has been suggested that the "Eiporen" in the walls of the medullary ray cells of *Pinus* are especially favourable for the protrusion of a tylosis, but this explanation loses its force when we consider the fact that in *Quercus alba* and *Robinia pseudacacia* the pits on the

¹ Jeffrey, E. C. The Comparative Anatomy and Phylogeny of the Coniferales, Part 1. The genus *Sequoia*. Mem. Boston Soc. of Nat. Hist. 5; X., pp. 441—459, Pls. 68—71, 1903.

² Conwentz, H. Ueber Thyllen und Thyllenähnlichen Bildungen. Berichte d. deut. bot. Ges. VII., pp. 34—40, 1889.

walls of the vessels are very small—from one-third to one-half the diameter of the Eiporen of *Pinus strobus*, and moreover provided with a narrow slit-like mouth—yet tyloses are so abundant that they completely fill the cavity of these vessels. The obscurity of the causes leading to the production of tyloses is shown by the fact that they are plentiful in *Quercus alba*, but scarce or absent in *Q. rubra*, although the size of the pits is practically the same in the two species.

Expressed briefly, this investigation goes to show that tyloses occur in the heart wood of the root and in the cone axis of members of the genus *Pinus*. In these places tyloses appear to be of normal occurrence, but their formation may be induced by wounding. It is suggested that these facts may provide an additional reason for considering *Pinus* to be an ancient genus.

Closely akin to tyloses are the proliferations from cells of the "Lückenparenchym" (Russow¹) into the cavities left by disintegration of the protoxylem elements. These have been reported by various authors as occurring in a number of ferns belonging to diverse families.² I have confirmed the presence of these growths in the stem of *Pteris aquilina*. They cannot be regarded as true tyloses, for they do not occupy the lumen of a vessel or tracheid, but are evidently similar in nature. Their occurrence is of interest in view of the reporting by Williamson and by Weiss of tyloses in the tracheids of fossil ferns.

¹ Russow, Vergl. Untersuch. d. Leitbündel Krypt. Mém. de l'Acad. Imp. de St. Pétersbourg 7 ; 19 : 80. 1871.

² See especially Prantl, Unters. z. Morph. d. Gefässkryptogamen. II. Schizaeaccen. Leipzig, 1881. Gwynne-Vaughan, D. T. Observations on the Anatomy of Solenostelic Ferns, I. Loxsoma. Ann. Botany, 14 : 87, 1901. Boodle, L. A. Comparative Anatomy of the Hymenophyllaceæ, Schizaeaceæ and Gleicheniaceæ, II., Ann. Botany 14 : 394, 1901.

EXPLANATION OF PLATE V.

- Fig. 1. *Pinus austriaca*. Tangential section through heart wood of the root. Tyloses are seen in connection with three medullary rays. × 100.
- Fig. 2. Same. One medullary ray with the initial stages of tyloses. × 200.
- Fig. 3. *Pinus strobus*. Transverse section through heart wood of root. Proliferations from medullary ray cells into adjoining tracheids. × 160.
- Fig. 4. *Pinus palustris*. Transverse section through cone axis. Tyloses are filled with a black substance. × 100.
- Fig. 5. Same. Tangential section through heart wood of root. Empty tyloses and their connection with medullary ray cells. × 45.
- Fig. 6. *Pinus ayacahuite*. Tangential section through cone axis. Several tyloses, one of which has passed through a pit from one tracheid to another. × 125.

A CONTRIBUTION TO VEGETABLE TERATOLOGY.

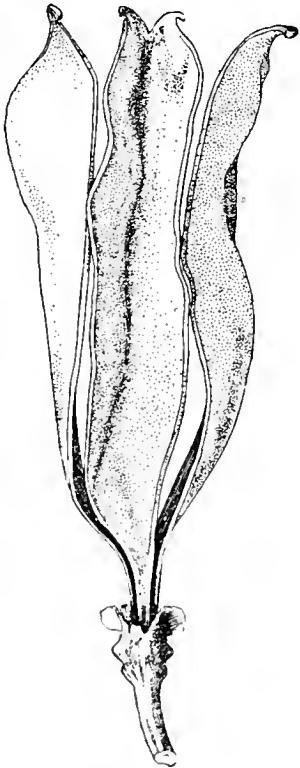
BY A. D. DARBISHIRE,

Royal College of Science, London.

[WITH TEXT FIG. 27].

THERE is a generally felt suspicion that many of the abnormalities which figure as instances of discontinuous variation are not of a blastogenic nature, that they are the result of injury or interference, and that they are not inherited. The opportunity of testing the latter point in a particular instance has presented itself to me.

The abnormality in question was exhibited by a pod of *Pisum Sativum* and was borne on some hybrid plants, of the F₄ generation, grown from seeds kindly given to me by Mr. C. C. Hurst. The number of pods, in this particular experiment, which passed under my eye was 3,833. This alone is sufficient to show that the abnormality occurs very seldom. I have, at other times, examined a very much greater number of pods than this, but I have not seen another example of this monstrosity.



Text Fig. 27. Abnormal pod of *Pisum sativum*. Natural size.

The abnormality (see accompanying figure) consists in the presence of a third valve, which is interpolated between the dorsal edges of the normal valves of the pod, *i.e.*, between the edges opposite to those to which the seeds are attached. Looked at from its outer surface, this third valve appears almost flat at its basal end. If we carry the eye slowly to the free end of the valve, we

very soon see a shallow channel appearing at its right hand border: this channel very quickly travels towards the middle of the valve, and, as it proceeds thence to the free end of the valve, it becomes gradually deeper and its sides gradually steeper until, at the very end, the two sides of the valley part, and end in separate points. At its basal end the whole pod may therefore be said to be triple, at its free end, on the other hand, quadruple.

The abnormality is not inherited. The abnormal pod, which was borne on the 14th¹ node of the plant, contained two seeds; these, together with seeds from all the other pods borne by the plant (*viz*: pods borne at nodes 13, 15, 16 and 17) were sown. They gave rise to 16 plants which bore 215 pods, all of which were normal. Details concerning the offspring of the plant bearing the abnormal pod are given in the accompanying Table.

¹ The point of attachment of the cotyledons is counted as the first node.

Node of Parent Plant.	Number of seeds in pod at that node.	Number of seeds sown.	Number of plants produced	Number of pods on individual plants, a, b, c, etc.
13	4	4	3	{ a. 13 b. 10 c. 10
14†	2	2	1	a. 12
15	5	3	3	{ a. 25 b. 15 c. 14
16	8	4	4	{ a. 6 b. 9 c. 13 d. 5
17	6	5	5	{ a. 20 b. 18 c. 15 d. 7 e. 23
	25	18	16	215

† The abnormal pod.

THE
NEW PHYTOLOGIST.

VOL. VII., Nos. 9 & 10.

DECEMBER 31ST, 1908.

EDITORIAL.

WITH the publication of the present issue the NEW PHYTOLOGIST completes its seventh year. The journal has met with much kindly support and encouragement from many quarters during its existence (it has even received the honour of parody), and the Editor believes that it fills, even if at times unworthily, a distinct place in the periodical literature of Botany.

But the hopes and ambitions expressed in the two editorial articles which appeared in the first volume (Vol. I., pp. 1, 221) have in many respects not been fulfilled. It has become clear, for instance, that British botanists will not carry on discussions on any subject in the pages of a journal. Whether this is a good or a bad thing for the progress of the science need not be discussed; it is evidently a firmly planted characteristic.

The Editor is also rather ashamed of his inability to obtain more than very occasional notices of important current literature. Such notices were originally intended to form an important feature of the journal, but no method that has hitherto been available has succeeded in securing them in sufficient number. The Editor is now, however, fortunate in being a member of a fairly large botanical staff, the *personnel* of which represents a number of different branches of the science, and he has been able to secure general assent to a scheme by which notices of current work

contributed by the different members of the staff of the Cambridge Botany School will become a regular feature of the *NEW PHYTOLOGIST*, beginning with the new volume in January, 1909.

At the same time the journal will be enlarged so as to contain at least 36 pages in a single number, that is, a minimum of 360 in the annual volume. It has from the outset been the Editor's desire to increase the size of the monthly issue, and thus to secure a better balance between different parts of the subject, but it is only quite recently that contributions have been received in sufficient number to justify such a course.

The price of the journal will be raised, to correspond with its increase in size, to fifteen shillings for the annual volume, and two shillings for each single number. It is hoped and believed that there will be more than a corresponding increase in the value of the periodical.

In conclusion the Editor desires to express his very cordial thanks to all his contributors and subscribers during the past seven years, and his hopes that the *NEW PHYTOLOGIST* will now enter upon an era of increased usefulness and increased circulation.

THE ANATOMY OF *SAXEGOTHÆA CONSPICUA* LINDL.

BY W. STILES, B.A.

(*Late Scholar of Emmanuel College, Cambridge*).

[TEXT-FIGS. 28—34]

INTRODUCTION.

THE Coniferous genus *Saxegothæa* contains one species, *S. conspicua*, found native only in wet woods on the upper slopes of the Andes of Chili, where it was discovered by William Lobb, a collector for Messrs. Veitch, who brought it to this country in the year 1849. In its native habitat it is a tree of Yew-like habit growing to a height of from twenty to thirty feet; in cultivation in Europe it forms a low bushy or shrubby tree¹. Owing to the fact that the attempts to cultivate it in this country have not been very successful, only a few plants of any size exist in Britain.

The vegetative parts of the tree, as already indicated, have the external appearance of those of *Taxus*, but, on the other hand, both the micro- and megasporangia are borne on sporophylls arranged spirally in cones.

The plant was first described and named in 1851 by Lindley², who regarded it as exhibiting a transition from the *Taxaceæ* to the *Pinaceæ*, with marked relationships to *Podocarpus*, *Dacrydium* and *Agathis*. Under the name of *Squamataxus Albertiana* it was described by Nelson³ writing under the *nom-de-plume* of "Senilis." From the first, the plant has been regarded as a species of a monotypic genus of the *Podocarpeæ*, although Carrière⁴ classed it as an anomalous genus of doubtful position.

Several short notes on the external features have been published by Masters⁵ which to some extent amplify Lindley's original description. Later accounts of the plant occur mostly in horticultural or systematic works, the most complete of these being found in Veitch's *Manual of the Coniferæ* and in Pilger's *Mono-graph in Engler's Pflanzenreich*.⁶ A few words by Bertrand and Bernard on the internal structure of the leaf, a description of the

¹ Veitch's *Manual of the Coniferæ*, p. 158, London, 1900.

² Lindley, J. (17), p. 258; (18), p. 111; (19), p. 229a.

³ *Senilis*, J. (26), p. 168.

⁴ Carrière, E. A. (8), p. 683.

⁵ Masters, M. T. (20), p. 684; (21), p. 782; (22), p. 246; (23), p. 10.

⁶ Pilger, R. (25), p. 42.

male cone by Thibout, a short reference to the plant by Spiess¹, and an account of the wood by Beust, referred to by Gothan², appear to complete the literature relating directly to the genus³.

For the material on which the following account is based, I have to thank Mr. H. M. Imbert-Terry, of Strete Raleigh, Exeter, who possesses two of the few trees of any considerable size in Great Britain.

THE STEM.

The stem has a central pith consisting of rather thick-walled loosely-packed cells, and xylem and phloem arranged as in all Conifers. In the cortex just outside the phloem is a ring of resin-canals of the usual type, each canal corresponding apparently to one of the primary vascular bundles. In older stems, certain cells, occurring singly or in groups in the cortex and pith, have their walls considerably thickened.

The tracheids of the secondary xylem, at any rate in plants grown in England, are small, with uniseriate pitting on the radial walls. Beust⁴ found that the pits are somewhat Araucarian in character, inasmuch as they are flattened horizontally. Gothan⁵ finds this is

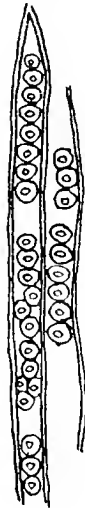


Fig. 28. Tracheids in the stem in longitudinal tangential section shewing a suspicion of the Araucarian type of pitting. $\times 300$.

also the case in several species of *Dacrydium*, where the pits are two-ranked and alternate, being therefore still more Araucarian than those of *Saxegothæa*. I have found in *Saxegothæa* an

¹ Spiess, K. von (28).

² Gothan, W. (13), p. 57.

³ Since this paper was written my attention has been called to a recent contribution by M. Tison on "Le nucelle stigmatifère et la pollinisation chez le *Saxe-Gothæa conspicua*," *Comptes Rendus CXLVII.*, p. 137, July 1908.

⁴ Beust (6).

⁵ Gothan, W. (13), p. 57.

occasional tendency to a two-ranked arrangement of the pits, and in these cases the pits tend to become alternate and hexagonal (Fig. 28). Resin-canals were not found in the wood.

The medullary rays are never more than one cell wide as seen in transverse sections of the stem, while longitudinal sections, of young stems at any rate, shew that they are rarely more than three cells deep. Beust has remarked, and Gothan confirmed, the peculiar simple pits on the horizontal walls of the cells of the medullary ray, as well as the fact that the tangential walls of the ray-cells are unpitted. As these writers state, *Saxegothæa* shews an approach to *Cupressinoxylon*¹ as regards the medullary rays.

THE LEAF.

The leaf appears to show no peculiarities of anatomical interest. Its structure was investigated by Bertrand², who stated that it closely resembled that of *Podocarpus*, except for the smaller quantity of transfusion tissue near the single vascular bundle. This transfusion tissue increases in amount towards the tip, and has been figured by Bernard³. As in Conifers generally, the leaf-trace is single, being accompanied by a single resin-canal on the outside of the phloem.

THE MALE CONE.

The male cones, which are of a reddish-brown colour, and about seven or eight millimetres long, are borne on short stalks in the axils of foliage leaves so as to form a raceme; they have been figured by Lindley⁴, Masters⁵, and Thibout⁶, but the figures of the first named writer are very unsatisfactory, while those of Masters shew little detail. There is generally only one cone in the axil of the leaf, but as Thibout states, there may be two or three. In the material at my disposal branched cones were numerous, but shewed no peculiarity of structure beyond the dichotomous branching of the vascular system.

The axis of the cone bears a number of spirally-arranged appendages, each of which consists of a pedicel containing a small vascular bundle and terminating in a short rather obtuse tip, while

¹ Barber, C. A. (1), p. 329. See also Lignier, O., "*Végétaux Fossiles de Normandie*, IV., p. 266, 1907.

² Bertrand, C. E. (5), p. 69.

³ Bernard, C. (4), p. 293.

⁴ Lindley, J. (18), p. 111; (19), p. 229b.

⁵ Masters, M. T. (21), p. 782.

⁶ Thibout, E. (29), p. 179.

on either side it is produced into a membranous lamina, to the lower side of which are attached the two microsporangia, one on each side of the sporophyll axis. The cone is surrounded at the base by an involucre-like ring of acute scales, each containing a vascular bundle and resin-canal similar to those of the leaf.

The axis of the cone contains a ring of small collateral bundles, the most internal elements being frequently separated from the rest of the xylem. The presence of these few scattered tracheids points to the occurrence of centripetal xylem. As usual there is a resin-canal outside the phloem of each bundle.

The bundle of the sporophyll is given off from one of the axial bundles by division of the latter in a tangential plane. It is very small and consists largely of phloem, only a single tracheid or two, or three tracheids at the most, being present in the pedicel. The bundle is accompanied by a resin-canal on the under or phloem side. The wall of the sporangium is one cell wide in the mature cone except on the outside of the latter, and the vertical cell walls are rather thick (Fig. 29). The wall is strikingly similar to that of

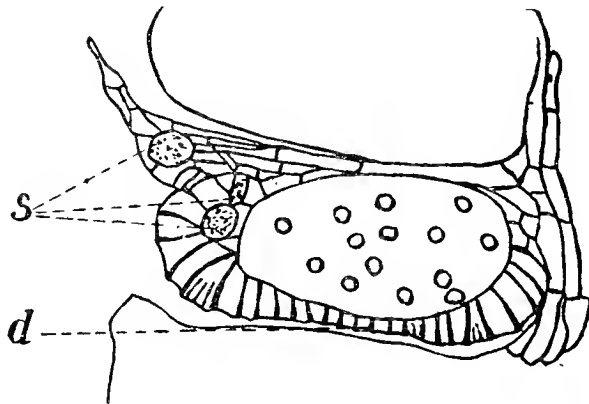


Fig. 29. Vertical section through a male sporophyll, not median. $\times 80$. *d*, point where the section cuts the line of dehiscence of the sporangium; *s*, large cells with deeply-staining contents between the outer wall and the tapetum.

Araucaria Rulei, figured by Seward and Ford¹, while the large secretory cells of the latter between the wall and tapetum, strongly suggest the large cells with deeply staining contents occupying a similar position in *Saxegothæa* (Fig. 22*s*). Dehiscence of the sporangium takes place transversely by means of a slit on the lower surface; its position is cut across transversely in Fig. 29 at the point *d*. On the splitting of the wall the part on either side of the slit rolls back so that at first sight the sporophyll appears to end in a large reflexed tip as described by Lindley². This writer's

¹ Seward, A. C. and Ford, Miss, S. O. (27), p. 356. Fig. 22*H*.

² Lindley, J. (18).

figure in Paxton's "Flower Garden" and on p. 229b of "The Vegetable Kingdom" shews the general appearance of the cone after the dehiscence of the sporangia, while his figure of the sporophyll shews two pollen-sacs present on a scale with the long reflexed tip caused by their dehiscence, which is, of course, incorrect. Both Lindley and Thibout decide that the male cone is very similar to that of *Podocarpus*. It appears also to shew some points of resemblance with *Araucaria*. As in the latter genus the pollen grains are not winged, in which respect they differ from those of *Podocarpus*.

THE FEMALE CONE.

The female cones are terminal on somewhat elongated branches, and consist of globular heads of spirally-arranged ovate-lanceolate imbricate ovuliferous scales (Fig. 30). The cone-bearing branch



Fig. 30. Branch bearing a female cone. $\times 2$. (For this drawing I am indebted to Mrs. Seward).

bears on its lower part several spirally-arranged leaf-like bracts which graduate into the ovuliferous scales. Each of the latter bears a single inverted ovule in a slight depression on the upper surface at a point nearer the insertion of the scale than the tip. The nucellus is enclosed in two integuments, the outer being loose and not so long as the ovule, the inner being of a firm texture and completely enclosing the nucellus, except at the micropyle, where a large part of it is extruded (Fig. 31), as is also the case in *Araucaria*.

It is noteworthy that the projecting apex of the nucellus is more prominent than in *Araucaria*; its great width and uneven surface are striking features in which it resembles the stigma of an Angiosperm.¹

The material examined by me had reached a stage in which a cavity, possibly the embryo-sac, had appeared in the middle of the nucellus (Fig. 31*c*). The cells in its neighbourhood are grouped more or less concentrically round it, while in the micropyle they are

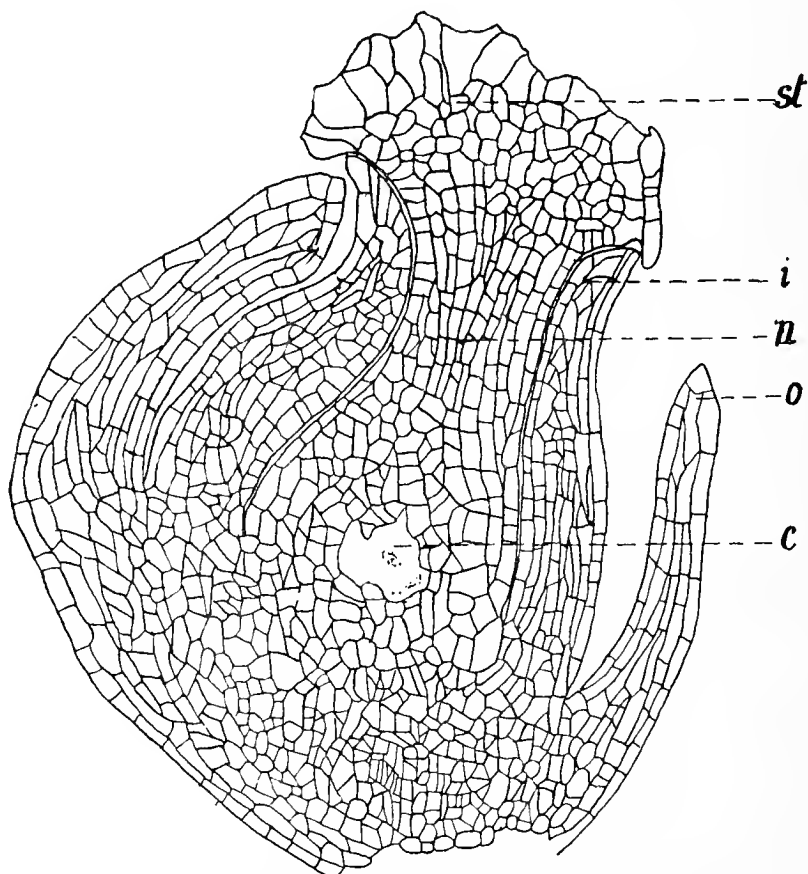


Fig. 31. Longitudinal median section through the ovule. *o*, outer integument; *i*, inner integument; *n*, nucellus; *st.*, nucellus extruded; *c*, central cavity.

somewhat lengthened longitudinally and often shew remarkable thickening bands on their walls; the cells of the stigma-like expansion are not so regularly arranged. It is hoped to continue the study of the megasporangium in the future when more material may be available.

After fertilisation the scale swells up and becomes fleshy, and, by the fusion of the scales of the cone, a globular fleshy mass is produced, containing the shiny pale brown seeds.

¹ M. Tison (l.c.) finds that the projecting apex is covered by a sticky secretion and presumably acts as a stigma; and also that it continues to grow in size for about two months after pollination.

At its base the axis of the female cone shews in transverse section a ring of about eight or nine bundles, endarch and collateral, enclosing a solid pith of rounded rather thick parenchymatous cells. On the outer side of the phloem of each bundle is a large resin-canal, as large as, or larger than, the bundle itself. As the apex of the cone is approached, the bundles begin to diminish in number, and grow gradually fewer, until near the apex of the cone they are reduced to two or three.

Below the insertion of a scale of the cone, one of the bundles divides in a tangential plane into a larger and a smaller bundle, while a short distance higher up this is followed by the division of the resin-canal into two equal canals. The larger bundle with its resin-canal then bends up through the cortex into the scale, while the smaller continues its course up the main axis, where it ultimately dies out, sometimes dividing again and giving off the bundle of another scale.

The vascular bundle of the scale continues at first in an almost

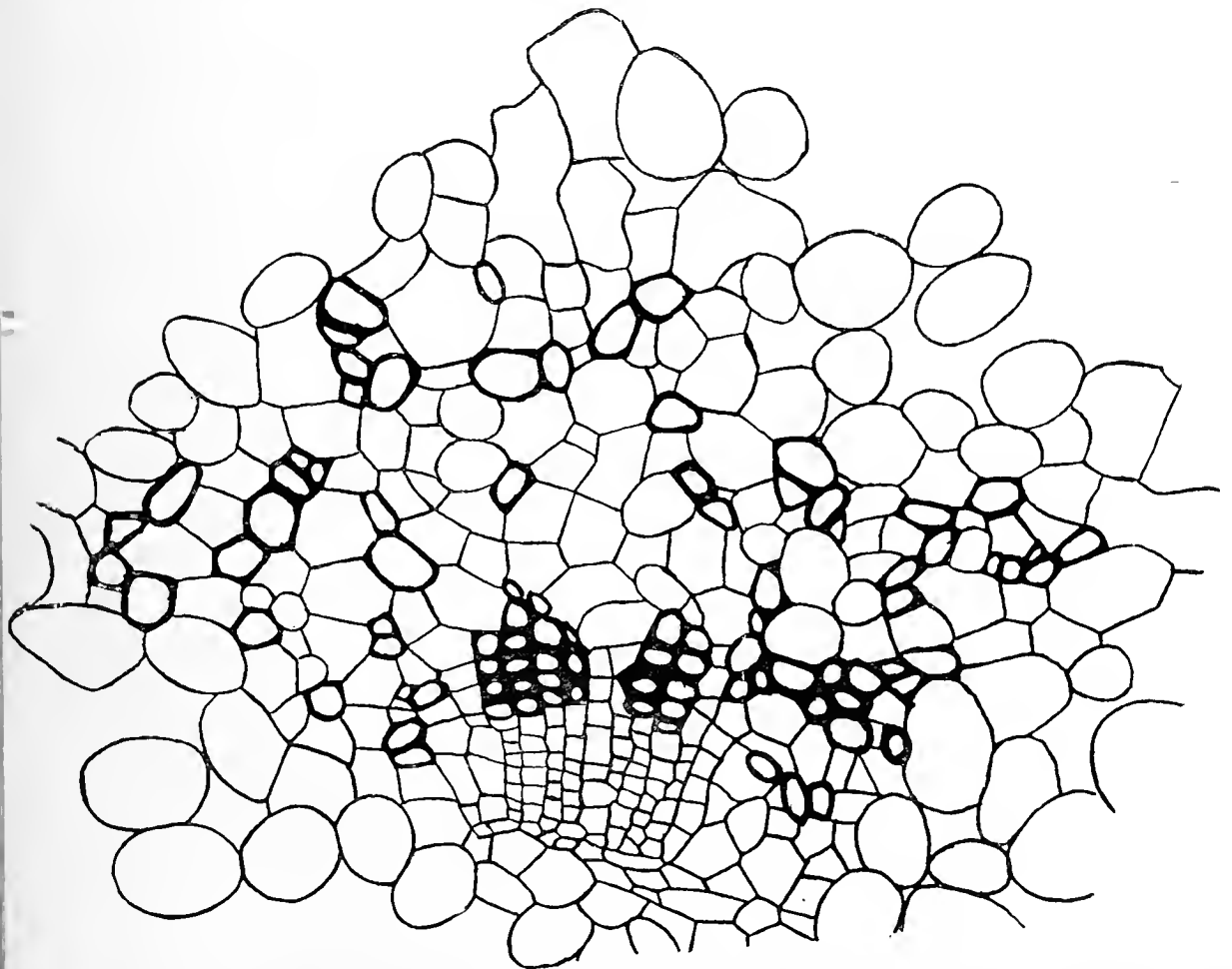


Fig. 32. Transverse section of the bundle of the female sporophyll towards the tip. $\times 500$.

vertical direction through the cortex of the axis, but soon bends outwards into the scale. Shortly after entering the tissues of the latter, two small strands are given off from the middle of the bundle on its upper side. The lower bundle supplies the scale, the upper bundles, which have their xylem and phloem with reversed orientation, supply the sporangium. The resin-canal does not divide, but remains

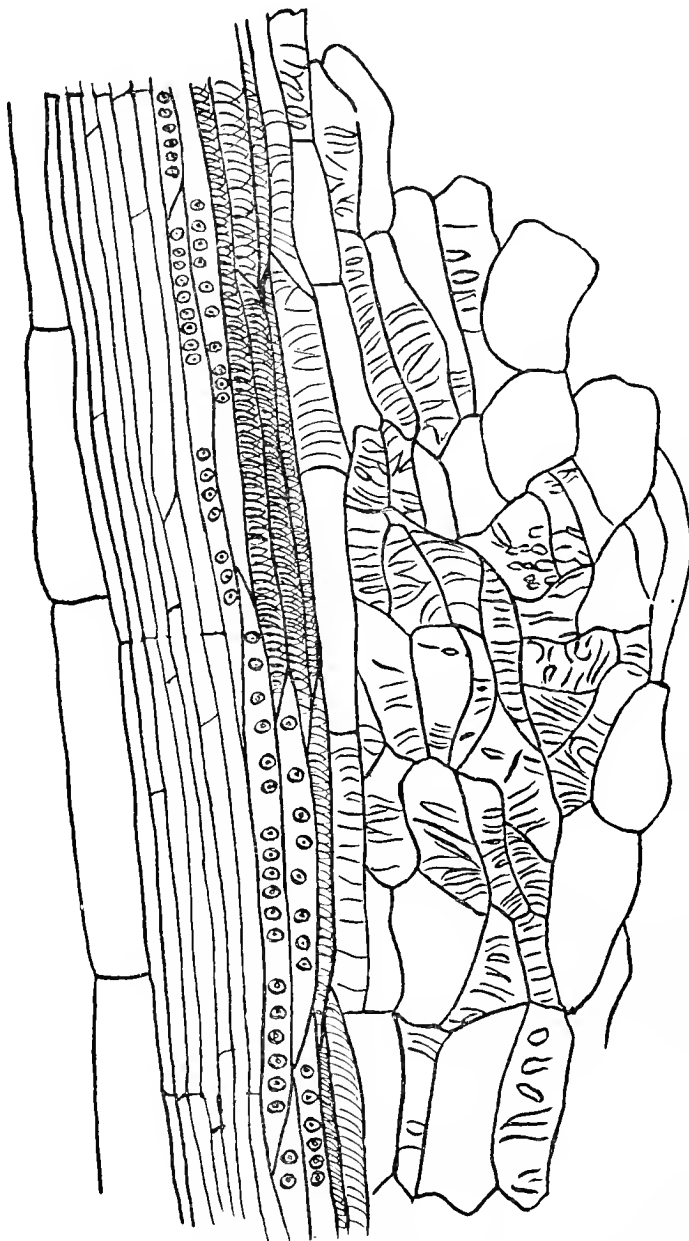


Fig. 33. Longitudinal section of the same. $\times 500$.

on the lower side of the larger bundle; the smaller bundles have no resin-canal. After this first bifurcation the lower bundle splits more or less into a row of smaller bundles, those at the end of the row on either side bending round so as to lie in, and form part of, the upper row. The remaining bundles of the lower row now join up into a single bundle with several short tracheids scattered in the

parenchyma on either side of the xylem and on the upper side of the scale (Fig. 32). They increase greatly in number towards the tip and no doubt constitute a large development of centripetal xylem. In longitudinal section they appear as short reticulately thickened elements, and are apparently of the nature of typical transfusion tissue (Fig. 33).

Meanwhile the bundles in the upper row, besides increasing in number by the additions from the lower row, become more numerous by division of one or both members of the original pair, and by fresh bundles arising in, or at the end of, the row. Their xylem consists almost wholly, or wholly, of centripetal wood. As the bundles increase in number, so in a similar way they diminish, by the fusion of two or more bundles, and by the dying out of others. Occasionally bundles occur ending blindly in both directions. The remaining bundles, about three in number, bend round to, and enter the sporangium, and in so doing follow a semi-circular course (Fig. 34b).

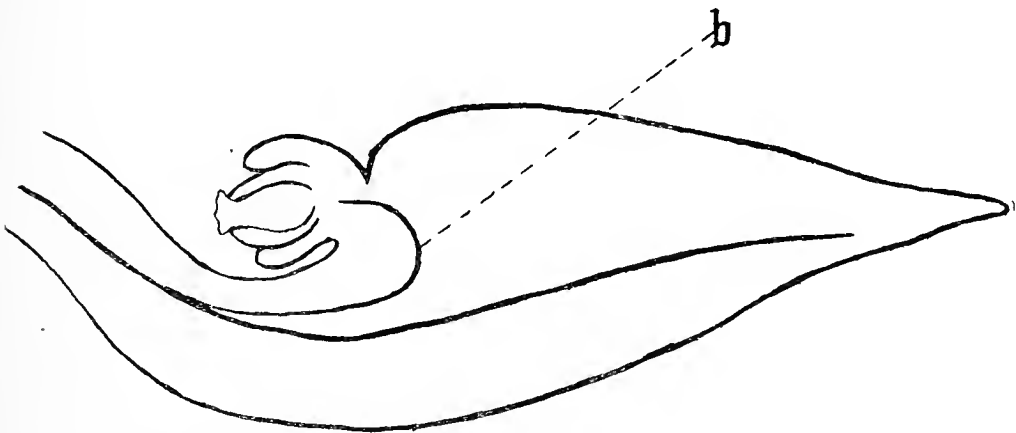


Fig. 34. Diagram shewing the course of the bundles in the female sporophyll as seen in median longitudinal section. *b*, bundle serving the sporangium.

There can be little doubt that the female organ of *Saxegothæa* resembles those of the *Araucariæ* more closely than it resembles those of other *Conifers*. The only other plants it shews close relationships with are the remaining *Podocarpeæ*. In the first place it agrees with the *Araucariæ* in having its megasporophylls arranged in a cone, and in both *Saxegothæa* and *Araucaria Rulei* there is a gradual transition from the foliage leaves to the cone-scales. The method of branching of the vascular bundles in *Araucaria Cookei*¹ and *A. Rulei*² is in the main very similar to that of *Saxegothæa*, the chief differences being that, firstly, in the latter the scale-trace bundle does not branch until it enters the tissues of

¹ Worsdell, W. C. (31), p. 527.

² Seward, A. C. and Ford, Miss S. O. (27), p. 361.

the scale, while in these species of *Araucaria* the first bifurcation takes place in the cortex of the cone axis; and, secondly, the bundles of the upper row do not bend round to the sporangium in *A. Cookei* and *A. Rulei* as they do in *Saxegothæa*. The vascular system in *A. Bidwillii* and *A. imbricata* is developed less like that in *Saxegothæa*, but in the former Worsdell¹ observed strands of phloem-like tissue entering the chalazal end of the ovule. The method of branching of the bundles in *Agathis*² is different, in that the single bundle divides into a row of about twelve, and then the median one of these gives rise to the upper row. Transfusion tissue is prominent in both *Saxegothæa* and the *Araucariæ*. It is of importance to note that in both cases also a portion of the nucellar tissue projects through the micropyle. On the other hand, *Saxegothæa* differs from the *Araucariæ* in having the ovule inverted³; it further differs from *Araucariæ* in not having the sporangium immersed in the tissues of the scale, and in the absence of a ligule, in which respects it agrees with *Agathis*.

Saxegothæa differs from all other *Podocarpeæ* except *Microcachrys tetragona* in having its female sporophylls arranged in a cone. The arrangement of the vascular bundles in the scale of *Microcachrys*⁴ is not unlike that of *Saxegothæa*, but more closely resembles *Araucaria Bidwillii*. The mode of attachment of the ovule in *Microcachrys* is also not unlike that of *Saxegothæa*. Transfusion tissue is also present in the female sporophyll of *Microcachrys*, but is wholly lateral in position.

The presence of only one resin-canal in the female scale of *Saxegothæa* is interesting, as in all other parts of the plant a single canal accompanies each primary vascular bundle on the phloem side. If the scale of *Saxegothæa* were a double leaf-structure it would not be unreasonable to expect to find two resin-canals, one on the phloem side of each bundle. The state of things found apparently indicates that the scale of *Saxegothæa* is what it at first sight appears to be: a simple sporophyll bearing on its upper surface a single megasporangium.

¹ Worsdell, W. C. (31), p. 532.

² Seward, A. C. and Ford, Miss S. O. (27), p. 360.

³ M. Tison finds that the ovule of *Saxegothæa* is at first perpendicular to the scale, but my material was not young enough to shew this.

⁴ Worsdell, W. C. (31), p. 537.

CONCLUSION.

In *Saxegothæa conspicua*, then, we have a plant somewhat isolated from others so far as the sum of its characters is concerned. Its distribution is extremely local since it occurs only in the Andes of Chili. Plants thus characterised are generally regarded as ancient types and relics of a past flora. This view is supported in the case of *Saxegothæa* by the internal structure. The structure of all parts of the plant described are remarkable for their simplicity as compared with other Conifers. The simple structure of the wood and medullary rays of the stem, the leaf with a structure shared by many other Conifers in different groups, the simple arrangements of the sporophylls and sporangia in the male and female cones, can hardly be all due to reduction, and together suggest that this plant exhibits primitive coniferous characters.

As regards its relations with other plants, the secondary wood is suggestive of the Araucariæ, the male flowers show points of resemblance with this order of Conifers, the pollen-grains of both *Saxegothæa* and the Araucariæ are not winged, and the female flowers of *Saxegothæa* are very like those of *Araucaria* on a smaller scale.

On the other hand the leaf of *Saxegothæa* is like that of *Podocarpus*, but as Conifers from different groups shew this type of leaf, it is probably not such a sure indication of relationship as the male cone. The close resemblance between this organ in *Podocarpus* and *Saxegothæa* is a reason against the removal of the latter from the Podocarpeæ to the Araucariæ. On the other hand, the pollen-grains are not winged as are those of *Podocarpus*.

As regards the other Podocarpeæ, *Microcachrys* resembles *Saxegothæa* in the female cone, and *Dacrydium* resembles it in shewing Araucarian features in the wood. All the Podocarpeæ have the solitary megasporangium inserted on the upper side of the scale in a reversed position, and there is a tendency throughout the order for the female scale to become fleshy after fertilisation. The Podocarpeæ therefore, as at present constituted, appear to form a natural group.

The few papers published on the Podocarpeæ deal mostly with the male gametophyte, and all these emphasize the fact that a small quantity of prothallial tissue is developed. In the first of these papers, Coker,¹ in 1902, after working on the gametophytes of a species of *Podocarpus*, came to the conclusion that the Podocarps

¹ Coker, W. C. (9), p. 89.

are most nearly related to the Abietineæ. Next, in 1907, Jeffrey and Chrysler¹ concluded that the Podocarps and Araucarians came from an ancestral stock closely allied to the Abietineæ. A little later in the same year, Miss Young² stated that "the rarity of any prothallial cells at all in Conifers, sets apart the Abietineæ, Podocarpineæ, and Araucarineæ, as the possible representatives of a more primitive condition. . . . A possible connection between the three groups is suggested. The question of relationships, however, can be answered only through the combined results of various lines of research." Lastly Burlingame³ apparently regards the Podocarpineæ and Abietineæ as derived from a common ancestral stock, and does not believe that the Podocarpineæ have come directly from the Abietineæ.

All these writers agree in the resemblance between the gametophytes of the Podocarpeæ and Abietineæ, but in the sporophyte of *Saxegothæa*, a member of the Podocarpeæ, it is hard to find a single character in which there is a greater resemblance to the Abietineæ, than to other Conifers. On the other hand the resemblance to the Araucarieæ is striking, a resemblance in which the gametophytes of *Podocarpus* and *Dacrydium* share. Unfortunately the state of the material at my disposal did not permit of an examination of the gametophytes, but the anatomy of the sporophyte would seem to indicate that *Saxegothæa* is an old type shewing relationships on the one hand with the Araucarieæ, and on the other with the Podocarpeæ. While we must wait for fuller knowledge before making any very definite statement, it would appear that these two orders of Coniferales are descended from some common ancestor with its micro- and megasporophylls both arranged spirally in cones. Along one line of descent we find the Araucarieæ, along the other is *Saxegothæa* leading on to *Microcachrys* and the other Podocarpeæ, and this view agrees well with the opinion of many botanists that the Araucarieæ are among the oldest, if not quite the oldest, Conifers. Thus it would seem probable, as Lindley said in his first description of the plant, that *Saxegothæa* is a transition of a remarkable kind between the Pinaceæ and Taxaceæ.

This investigation was undertaken at the suggestion of Professor Seward, whom I here wish to thank for advice during the work. I would also express my thanks to Mrs. Seward for the drawing of the female cone (Fig. 3).

¹ Jeffrey, E. C. and Chrysler, M. A. (16), p. 355.

² Young, Miss M. (32), p. 189.

³ Burlingame, L. L. (7), p. 161.

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NOTES FROM THE CAMBRIDGE BOTANY SCHOOL; IV.

ON THE ANATOMY OF *DIOON EDULE*, LINDL.,

BY

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AND

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[WITH TEXT-FIGS. 35—40.]

GENERAL DESCRIPTION.

THE specimen on which the following account is based was grown for about thirty years in the Botanic Garden, which later became the White City, at Manchester; it was then transplanted to the Cambridge Botanic Garden, whence it was sent for our examination. Its approximate age was 120 years, and it had flowered only once under observation, at Manchester, when a female cone was produced. When cut down it was a small tree of 65 cms. in height, and 80 cms. in circumference including the leaf-bases, with which the trunk was thickly beset. Surrounding the apex was a crown of pinnate leaves, each about 135 cms. long. At 5 cms. above the ground a lateral bud was found; this had apparently aborted, for periderm thickenings had occurred in places, and a deposit of gum was present in spaces in the tissues. The trunk was sawn up, and dissections were made of some of the pieces. The mucilage and sap which exuded from the cut surfaces

of the plant turned a deep purple-red colour on exposure to the air. Previous to dissection the piece was boiled for some hours in order to soften the parenchymatous tissues of the cortex and medulla. Parts were preserved in spirit for the investigation of the minute anatomy; hand sections were cut and stained with iodine green and eosin.

ANATOMY.

I.—Vegetative Axis.

A transverse section of the stem shews a very large central medulla; this contains, as do all the other parenchymatous tissues of the plant, a great number of ramifying mucilage cells. Surrounding the medulla is the single vascular cylinder. This is a narrow zone of tissue, consisting of xylem, phloem and a middle layer of cambium; the average thickness of the vascular layer is $\frac{1}{2}$ cm., *i.e.*, about one-fifteenth of the radius of the stem. The vascular supply appears quite inadequate compared to the bulk of the stem (Figs. 35 and 36. *vas. cyl. I.*); but the slow rate of growth, the small number of leaves functional at one time, and the xerophilous habit, necessitate a much smaller conducting channel than is usual in the majority of plants. The vascular system is a coarse irregular reticulum, pierced by medullary rays of breadth varying from one to about ten cells.

From the protoxylems at the bases of the meshes of the network arise the leaf-traces (Fig. 35, *l.t. I.*); these pass out in the rays and take an oblique course in the vertical radial

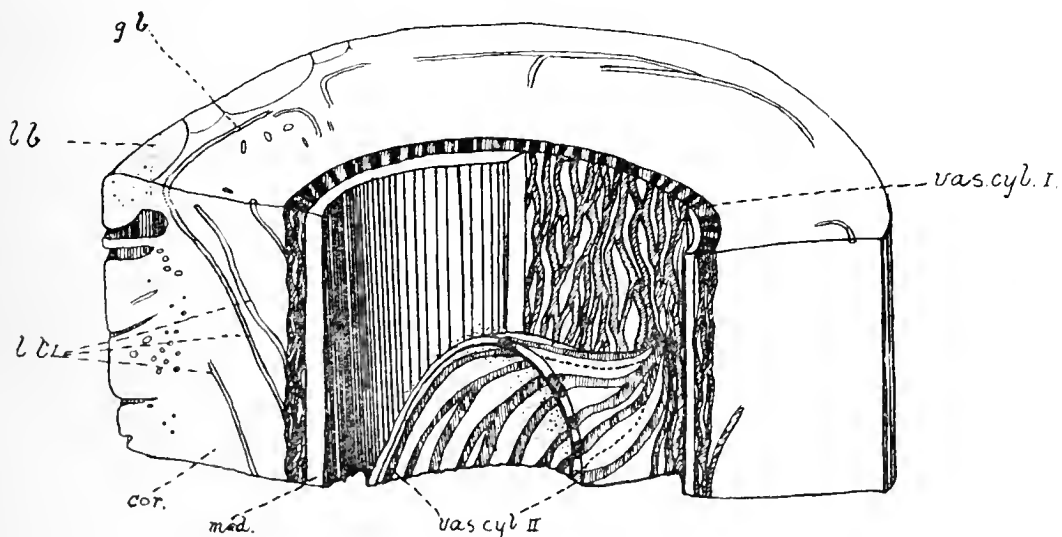


Fig. 35. Dissection of a hemi-cylindrical piece of the trunk; *vas. cyl. I.*, main axial cylinder; *vas. cyl. II.*, inner vascular dome passing into the peduncular cylinder; *l.t. I.*, leaf-trace from the main axial cylinder; *g.b.*, girdle-bundle; *l.b.*, leaf-base; *cor.*, cortex; *med.*, medulla.

plane for about 4 cms. and bifurcate; the two halves, then turning to right and left, girdle the stem horizontally. Sections of the cortical zone shew a great number of these girdle-bundles, two of which enter each leaf-base, from right and left; these quickly branch in the petiole to form the complicated system described by Mettenius¹.

At two points in the trunk, respectively 22 cms. and 48 cms. above the ground, a ring of bundles arises internally from the main cylinder, and pursues an oblique curving course in the medulla, with the result that a dome-like system of vascular tissue is produced (Figs. 35, 36, 38, *vas. cyl. II.*) As the dome contracts towards the top, the individual bundles anastomose, and eventually form a few broad strands arranged in a narrow cylinder. In this condition the vascular tissue bends over to one side; passing through a gap in the cauline cylinder, this peduncular cylinder—for such is its nature—bends slightly downwards and enters the cortex (Fig. 36, *ped. cyl.*) The base of the peduncle

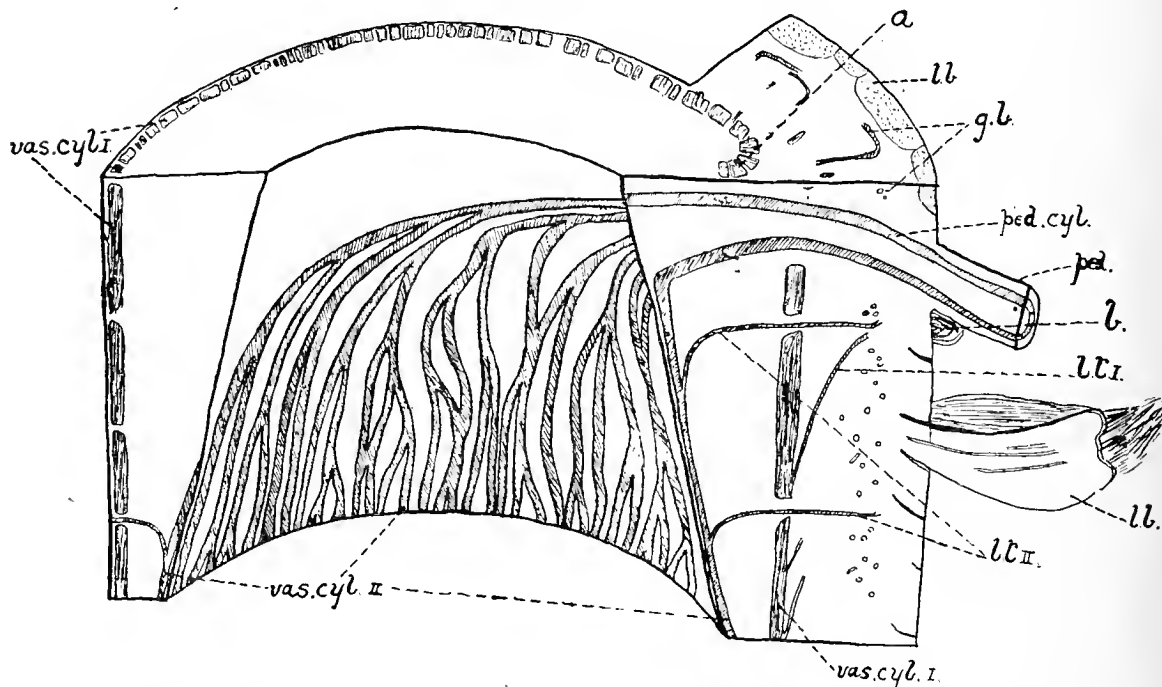


Fig. 36. Dissection of a hemi-cylindrical piece of the trunk, the vertical section passing through the point of egress of the peduncular cylinder. *l.t. II.*, leaf-trace from the inner dome; *ped.*, peduncle; *ped. cyl.*, peduncular cylinder; *a.*, incurved lip of *vas. cyl. I.* at point of egress of *ped. cyl.*; *b.*, aborted bud. Other letters as in Fig. 35.

remains in a somewhat crushed condition, projecting laterally from the stem and hidden by persistent leaf-bases. Close beneath the peduncle, but slightly to one side, a small aborted bud is

¹ Beiträge z. Anat. der Cycadeen; Abhandl. d. k. Sachs Ges. d. Wiss., 1860.

present (Fig. 36, *b*). The internal peduncular dome gives off in two irregular whorls a number of leaf-traces similar in origin and character to those from the cauline cylinder; these pass radially outwards through the main cylinder into the cortex, where they behave like the ordinary girdle-bundles (Fig. 36, *l.t. II.*)

This peculiar arrangement of the vascular tissues is clearly a result of the sympodial growth of the stem (see Figs. 37 and 38). The cone terminates the main axis, the dome-shaped vascular system being the normal condition at the stem apex. The main

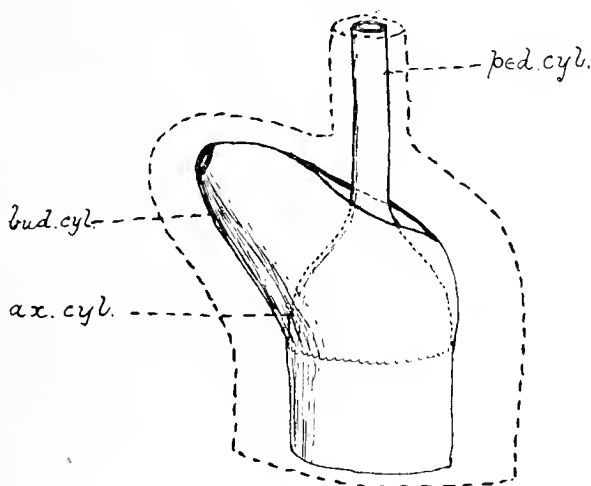


Fig. 37. Diagram representing the relation of the vascular system of the chief lateral bud to that of the primary axis and peduncle. *ax. cyl.*, the main axial cylinder narrowing into *ped. cyl.*, the peduncular cylinder; *bud. cyl.*, cylinder of the lateral bud which continues the growth of the trunk.

growth of the stem is continued by one of a pair of opposite lateral buds, the vascular tissue of which unites with that of the main axis in a horizontal ring; the upper surface of the vascular dome of the bud having a gap through which the peduncular cylinder, passes. Later, as the lateral bud becomes terminal by the increased growth of the under side, the peduncular cylinder, persisting after the cone has fallen, is thrust over to the side remote from that on which the bud originated; so that it even comes to slope downwards in the cortex. The vascular cylinder of the lateral bud increases greatly in size, and eventually appears continuous with the original cauline cylinder; the true apical dome remaining enclosed in what is now the main conducting cylinder of the trunk.

The aborted bud (Fig. 36, *b*) beneath the peduncle is the second lateral branch of the primitive dichasium, only one branch of which develops.

Figures 35 and 36 represent semi-diagrammatically dissections of two pieces of the trunk in the region where the internal cylinder

narrows, bends over, and passes out horizontally to the remains of the peduncle. The leaf-bases have for the most part been removed, and much of the parenchymatous tissue of cortex and pith has been dissected away, in order to expose the vascular skeleton.

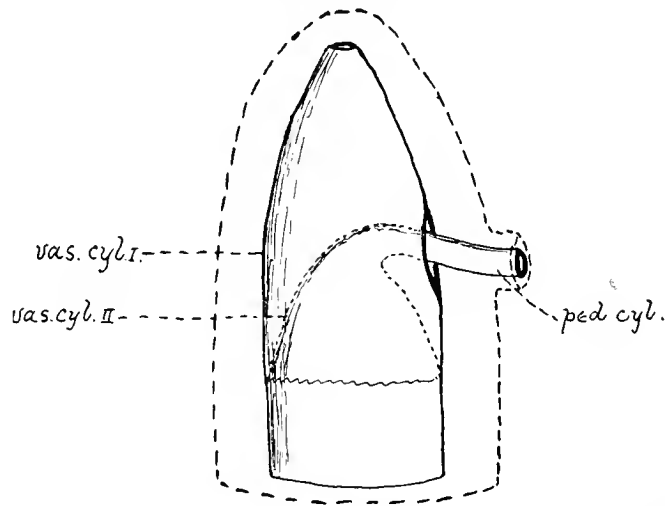


Fig. 38. Diagram of the vascular arrangement after the lateral bud has become terminal in position. Letters as in Fig. 2.

The minute anatomy of the vascular tissues is of the well-known type. The xylem of the axial cylinder consists of a very large number of radial rows of tracheids, mixed with uni- or bi-seriate rows of parenchyma, these continuing outwards through the phloem. The protoxylem and protophloem are in a crushed condition. The cambium is broad, and the processes of growth and lignification appear to be slow. Xylem and phloem are present in about equal bulk. Anomalous cylinders, such as are found in *Cycas*, *Encephalartos*, *Macrozamia*, &c., are absent; and bundles with inverse orientation appear not to be developed; there is no trace of the medullary vascular network so conspicuous in *Macrozamia* and *Cycas*¹. The stem structure thus approximates more closely to the type of *Stangeria paradoxa*².

II.—Peduncular Cylinder.

Where the main vascular system narrows into the peduncular cylinder (Fig. II., *ped. cyl.*) the bundles unite laterally: the main medullary rays become reduced in number, but the radial uni-seriate rows of parenchymatous cells persist. At the base of the peduncle, below the insertion of the sporophylls, the main vascular tissue is arranged in a regular ring of about five strands separated by medullary rays of about four cells broad. No trace of centri-

¹ Worsdell: Ann. Bot. X., p. 601, 1896.

² Solms-Laubach: Bot. Zeit., 1890, Nos. 12-15.

petal xylem can be detected in this position, this fact being in agreement with the condition found by Scott in *Stangeria*¹.

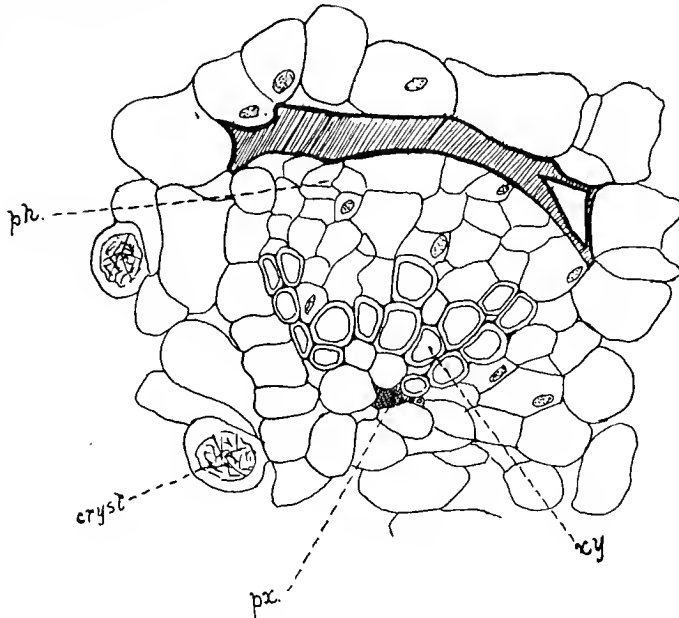


Fig. 39. T.S. collateral cauline bundle from cortex of base of peduncle. *xy.* xylem; *ph.* phloem; *px.* protoxylem; *cryst.* sphere crystal.

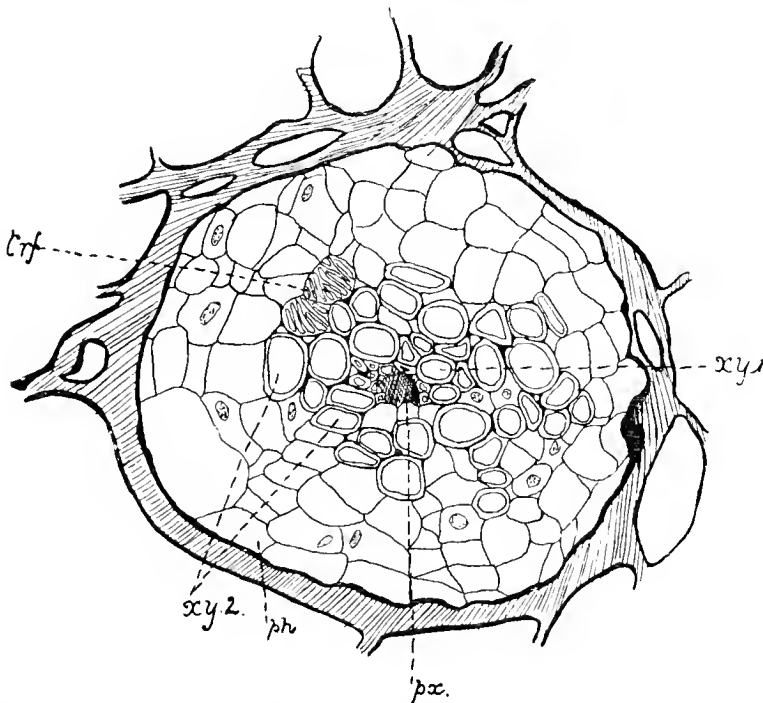


Fig. 40. T.S. concentric cauline bundle from the cortex of the base of the peduncle. *xy. 1.* primary xylem; *xy. 2.* secondary xylem; *trf.* transfusion tracheids. Other letters as in Fig. 39.

Higher up in the peduncle² centripetal xylem appears in the ill-marked perimedullary zone in quantity comparable with that in

¹ Ann. Bot. XI., p. 403, 1897.

² Owing to the absence of all but about 2 cm. of the base of peduncle, the investigation was continued on laboratory spirit-material of male and female cones.

*Stangeria*¹. In the fertile region of the axis centripetal wood dies out completely.

In the cortex of the base of the peduncle small bundles are found, as in *Stangeria*: these are sometimes collateral (Fig. 39), but irregularly orientated; frequently they are of concentric structure, the protoxylem being central, and secondary growth proceeding radially to a small extent all round (Fig. 40). In some a tendency to divide into two is noticeable. Scott is of opinion that the similar bundles in the peduncle of *Stangeria* are vestiges of the traces of missing leaf structures: this would appear to be also true of *Dioon*, as suggested by Matte².

III.—*Sporophylls*.

The quantity and distribution of the centripetal xylem in the male and female sporophylls has been determined by Worsdell³; our own observations exactly agree with his description. Stomata are thinly scattered over the surface of the broad part of the male and female sporophylls, and open into the usual air-chambers. The functions of these are probably rather those of transpiration and respiration than of assimilation, since the cuticle is of considerable thickness, and very few chloroplasts are present. The presence of stomata here furnishes no argument for either view as to the nature of the sporophylls, since they are known to arise independently on many different aerial organs.

IV.—*Roots*.

The roots arise adventitiously from the base of the stem, three or four of them being large and profusely branched. The smaller roots, which are long and but little branched, are covered with small nodules strongly resembling those found in the Leguminosæ; these occur either singly or to the number of four or five in a clump.

All the roots are diarch and contain a large amount of secondary tissue. Here and there in the cortex a considerable number of stone cells occur. The external layers are corky and are developed from the usual phellogen.

The nodules consist of parenchymatous cells, frequently containing crystals of various kinds and deposits of tannin. It is

¹ Scott, loc. cit., pl. XX., fig. 3.

² Recherches sur l'appareil libero-ligneux des Cycadacees, Caen, p. 115.

³ Ann. Bot. XII., p. 221 et seq., 1898.

possible that the young cortical cells immediately inside the phellogen contain the hyphæ of an endophytic fungus, or bacteria; these facts, however, could not be definitely determined, since the roots of the specimen examined were too long exposed before fixing, and consequently were in a bad stage of preservation. Should the suggestion prove to be correct it would fall into line with the facts observed by Life in *Cycas revoluta*¹. All that can be definitely stated at present is that these cells are in a distinctly disorganised condition, and that their contents are stained deeply with methylene blue.

GENERAL CONSIDERATIONS.

Dioon edule, so far as the anatomy is concerned, appears to occupy a place among living Cycads very close to *Stangeria paradoxa*; (i.) in the stem anatomy as described by Solms-Laubach; (ii.) in the amount and distribution of the centripetal wood in the peduncle; and (iii.) in the presence of cortical strands in the base of the peduncle.

The view that, in the majority of Cycads, the cone is terminal, is based primarily on the obviously apical position of the megasporophylls of *Cycas*, and on the peculiar disposition of the vascular tissues of the peduncular cylinder in *Stangeria*, which we have also found in *Dioon edule*. The presence of cortical cauline bundles in the peduncle seems to indicate that the cone was not always so sharply marked off from the trunk as it is at present in the majority of Cycads. The monopodial growth of the trunk in *Encephalartos Altensteinii* and other species² is clearly a later development, and is connected with the production of several cones simultaneously.

In conclusion we must express our thanks to Professor Seward for valuable help and suggestions throughout this investigation, and to Mr. Irwin Lynch for kindly giving information as to the history of the specimen.

¹ Bot. Gaz., XXXI., p. 265, 1901.

² Pearson. Trans. S. Afr. Phil. Soc., XII., p. 345, Dec., 1906.



THE PHYLOGENY AND INTER-RELATIONSHIPS OF
THE PTERIDOPHYTA.

BY LADY ISABEL BROWNE.

V.—FILICALES.

BOTRYOPTERIDEÆ.

IN the first two orders of Ferns to be considered here, the fossil Botryopterideæ and the Hymenophyllaceæ, we find exarch and endarch protostely. This makes it convenient to discuss the anatomy of the stem in both orders at the same time; but in so doing it is necessary to guard against prejudging the question of the degree of affinity between them. Dr. Scott divides the fossil order into the Botryoptereæ, in which the stele is more or less circular, and the Zygoptereæ, in which it is more or less deeply lobed. In the latter group, including the genera *Zygopteris*, *Asterochlaena*, and *Anachoropteris*, the stele consists of two kinds of wood, the so-called external and internal xylem. The former is larger-celled, except at the ends of the projecting arms or rays; but the inner part of the stele consists of parenchyma, embedded in which are groups of small tracheides (24). It is interesting to compare these more complex steles with those of *Botryopteris*, *Tubicaulis* and *Grammatopteris*, members of the Botryoptereæ. In *Zygopteris corrugata* we have a form possibly intermediate between the two types, for here we have the same groups of internal tracheides embedded in the parenchyma and surrounded by external xylem. But while the internal tissue forms angles projecting slightly into the external wood, the outline of the latter and of the stele remains circular, except just previous to the departure of the leaf-trace. As regards the position of the protoxylem, Miss Stopes, who investigated *Tubicaulis*, states that though the protoxylem is not particularly well differentiated, we may safely say that in that genus the whole, or nearly the whole, of the wood was centripetal (29). The Permian *Grammatopteris* was reported by Renault to have an exarch protostele, while *Botryopteris* is said to be endarch (24). Among the Hymenophyllaceæ, some species, e.g., *Trichomanes scandens*, possess an exarch protostele containing a few parenchymatous cells. Others, including *T. reniforme*, have a central protoxylem embedded in parenchyma and surrounded by two bands of tracheides.

In others, e.g., *T. spicatum*, the circular stele contains irregularly scattered small elements. In several species of *Trichomanes* and *Hymcnophyllum* the stele is sub-collateral, i.e., consists of a band of xylem surrounded by a layer of phloem occasionally interrupted on the lower side; in yet others the stele is truly collateral and the phloem is confined to one side of the xylem, the latter being often much reduced (3).

Mr. Tansley regards both the Botryopterideæ and the Hymenophyllaceæ as primarily endarch (31) (32); and Mr. Boodle, in discussing the anatomy of the Hymenophyllaceæ, selects as the primitive type the endarch stele of *Trichomanes reniforme* (3). Curiously enough Mr. Tansley selects as primitive in the Botryopterideæ the two genera reported to be exarch. He states that the solid cylindrical strand of tracheides devoid of parenchyma found in *Grammatopteris* and *Tubicaulis* is probably the most primitive type of vascular strand found in vascular plants (26). He claims that special protoxylem has not yet been detected in these types; but although no true spiral protoxylem has so far been found in them, there seems little reason to doubt Miss Stopes' report that the stele of *Tubicaulis* is nearly, if not quite, exarch (29). In *Grammatopteris*, although a re-investigation of the fossil is desirable, it would seem from the position of the protoxylem at the ends of the narrow band-shaped leaf-trace, that, at least at the insertion of the latter, the protoxylem of the stem must be nearly, if not quite, peripheral. Mr. Tansley points out that *Botryopteris* also has a solid stele, but that it contains fairly constantly a central strand of small tracheides probably representing protoxylem. In *B. (Rachiopteris) cylindrica* this central small-celled tissue, supposed to represent protoxylem, is usually remarkably clear, but preparatory to branching it divides into two groups. Mr. Hick records the fact that when four or five such groups occur, "as is often the case," they are arranged symmetrically around the centre as though they had originated by the division of a smaller number (19). This appearance cannot well be due to branching, as this species is known to have branched dichotomously. If Mr. Hick's description is exact the supposed protoxylem cannot, in these cases, have occupied a truly endarch position; its position would appear to be somewhat mesarch. But even after making allowances for all such possible exceptions the fact remains that *Botryopteris cylindrica* is typically endarch, and this is a strong point in favour of Mr. Tansley's view. But when he proceeds to argue, on grounds of wide anatomical

comparison, that endarchy is the primitive condition, it is more difficult to agree with him. He concludes that among Algæ and Bryophyta there is a tendency to develop conducting tissue at the centre of the axis; that the primitive protostele originated thus; and that if this strand became too bulky for its elements to develop simultaneously, the tendency for the more central ones to mature would still hold good, thus giving rise to endarchy. But in using comparative evidence the structure of the more primitive members of the other Pteridophytic phyla should be brought into consideration. Exarchy appears to be primitive in the Sphenophyllales, Psilotales and Lycopodiales, while traces of centripetal xylem have been found in an ancient member of the Equisetales. So that, *a priori*, we should expect the Ferns to be primitively exarch, since all Pteridophyta probably possess a common vascular ancestor. Though some botanists would deny this, few, if any, would deny the origin of Ferns and Pteridosperms from a common vascular ancestor. But it is among the Pteridosperms and allied forms that the gradual replacement of the primitive centripetal xylem by centrifugal wood is most clearly illustrated (23), (25), (26). Thus on comparative grounds there is a presumption that the Botryopterideæ were primitively exarch. This in no way invalidates the view that vascular tissue originated at the centre of the stem, since there are indications among the lower plants that this is so. But though the Botryopterideæ appear to be somewhat primitive Ferns there are few indications that they are such very primitive vascular plants. Mr. Tansley admits that their fronds are elaborate and highly evolved (31); they are often dimorphic, and in one genus, not yet fully described, a considerable amount of secondary xylem is present (24). Further, if exarchy is primitive it is easier to understand the structure of the stele in the Zygoptereæ, with its sharp differentiation into inner and outer wood, the latter presumably representing centrifugal xylem acquired later than and causing the reduction of the inner centripetal xylem. The outer wood is clearly not secondary, and if the inner wood developed centrifugally such a sharp line of demarcation between the two would be hard to understand.

HYMENOPHYLLACEÆ.

As regards the Hymenophyllaceæ, both Mr. Boodle and Mr. Tansley regard the type of stele of *Trichomanes reniforme* and of the larger Hymenophyllums as primitive for the order (3), (32). In this type the endarch protoxylem and a few other woody cells are

embedded in central parenchyma and surrounded by two bands of tracheides. Mr. Boodle admits that the species with larger solid steles, such as *T. scandens*, might be regarded as more primitive than the type of *T. reniforme*, but he claims that the sub-coriaceous fronds of many of them indicate that they have probably become adapted to less moist conditions, and that this has brought about the increase in the conducting elements of the stele (3). Mr. Boodle strongly supports the view that the Hymenophyllaceæ are reduced and that the filmy character of the leaf is due to reduction. It is therefore hard to see why the conducting elements should be more numerous, for example in *T. scandens* than in *T. reniforme*, the leaf of which may be called filmy, since it has no intercellular spaces, although it is several cells thick. But, as Mr. Tansley points out, the thickness of the leaf is a point in favour of the primitiveness of *T. reniforme* (32). It would seem more natural to regard the forms with solid steles, such as *T. scandens*, as relatively primitive. Such a type is usually regarded as highly primitive and is so considered by Mr. Tansley in *Tubicaulis* and *Grammatopteris*. Here, as in those genera, the solid stele is associated with exarchy, and such an association strongly favours the primitiveness of exarchy. There are, however, other species with solid steles that are not exarch, as for example *Trichomanes radicans*. Mr. Boodle asserts that *T. reniforme* appears to be more primitive than *T. radicans* because it has sori on most of its veins. But this character is not necessarily a primitive one; it might result from reduction of leaf-surface unaccompanied by decrease in the number of sporangia produced. Such reduction may well have occurred, since the leaf of this species is exceptional in being simple. Mr. Boodle accounts for the origin of the exarch stele by supposing that definite protoxylem having been lost, owing possibly to slow growth in length, a fresh protoxylem may have reappeared under other and more rapid conditions of growth in a different position. The difficulty that a change in the position of the protoxylem has occurred within the Hymenophyllaceæ must be faced; it would seem to be best met by Mr. Boodle's hypothesis. But this change of position of the protoxylem may equally well have resulted in the evolution of endarch types from exarch forms. This is what the present writer believes has occurred, not only in the Hymenophyllaceæ, but also in such of the Botryopterideæ as were really endarch. Mr. Tansley argues that the primitiveness of endarchy in the Hymenophyllaceæ is supported by its "apparently general

occurrence" in the Botryopterideæ; but, as already indicated, endarchy may well have been exceptional in that order. He also contends that the advantage of an early development of peripheral tracheides for the attachment of roots might become a factor in evolution, but that it is very hard to conceive of endarchy as the derivative condition. It has, however, already been recognized that centrifugal wood has frequently in the phylogeny supplanted centripetal xylem.

Mr. Boodle's view that the sub-collateral type of stele arose by reduction from the two-banded type of *T. reniforme* seems well-founded. He was able to show that in some species the larger examples are two-banded, and the smaller ones sub-collateral. Thus the available data tend to disprove the theory that the simple collateral types were primitive. Moreover it is clear that the truly collateral type of stele, *i.e.*, that in which the phloem is confined to one side of the xylem, arises by a continuation of the process of reduction by means of which the sub-collateral type was derived from the two-banded one. This is borne out by the fact that many of these species with collateral steles develop very little xylem (3).

Mr. Boodle considers it very probable that the Hymenophyllaceæ were derived from non-filmy ferns. This is strongly supported by the presence of pseudo-veins, devoid of vascular tissue, and by the facts quoted, showing that there has been a considerable reduction in the steles of many species. It is also borne out by the fact that the filmy habit appears to have arisen independently of the Hymenophyllaceæ in the Osmundaceæ. In spite of so many indications of reduction Professor Hallier regards the one-layered condition of the leaves of most Hymenophyllaceæ as primitive, not only for the order, but also for the phylum (18).

There has been much discussion as to whether the flat thalloid prothallus found in *Hymenophyllum* and some species of *Trichomanes*, or the filamentous and Alga-like one of other species of *Trichomanes*, is primitive for the order. Prantl and Goebel considered the filamentous form as primitive, and Sadebeck has recently re-stated this view, asserting that although there is in the order a beginning of the formation of a cell-surface, "... yet we see from the development as a whole that the filamentous form of prothallus is the original one for *Trichomanes*" (22). Professor Bower and Dr. Campbell, on the other hand, attribute to the filamentous prothallus a secondary origin from the thalloid type, and the latter states that its form is probably largely due to environment (12), (7). This view

is probably correct, being supported by the fact that the sporophyte is clearly reduced, and that the gametophyte has, as pointed out by Professor Bower, been exposed to the same conditions. Further, if the filamentous type were primitive we should expect to find it retained by primitive members of other filicinean orders. This latter argument is slightly weakened by the fact that filamentous prothalli have been found in two species of *Schizæa* (10), (38).

As regards the affinities of the Hymenophyllaceæ with the Botryopterideæ the two orders have much in common. This is true whether we select as primitive the forms with a solid exarch stele, or, in agreement with Mr. Boodle and Mr. Tansley, regard the endarch forms of both orders as primitive. In the former case there is a distinct similarity between the steles of *Tubicaulis* and *Trichomanes scandens*. In the latter case we have, as remarked by Mr. Boodle, an interesting likeness between *Zygopteris* and such a form as *Trichomanes reniforme*; in both we have small internal tracheides embedded in parenchyma and surrounded by vascular elements. The present writer holds that these structures arose in a different way: that the internal tracheides of *Zygopteris* represent the remains of centripetal xylem, and that its outer xylem was probably centrifugal; whereas *Trichomanes reniforme* arose (as the writer believes) by reduction from a form with a solid stele, its exarch ancestors having lost their protoxylem, which afterward reappeared in the centre of the stele. But it is possible, and many will think it probable, that both orders were primitively endarch. Then the resemblance of species of *Trichomanes* to *Zygopteris* is striking; it extends to the presence in many species of both genera, of an axillary shoot, whose vascular bundle is in both cases cut off from the leaf-trace in essentially the same way. The rarity of the axillary shoot makes it a character of importance; but it has been suggested by Mr. Boodle that this mode of branching may be a modified dichotomy, the undivided trace (as the trace is termed before giving off the bundle of the axillary shoot) representing the weaker branch of the dichotomy, that may be supposed to bear the apparently subtending leaf. If the axillary shoot with its leaf represents a modification of dichotomy, it may have arisen independently in the two orders, and not be proof of close affinity. Thus whether the endarch or exarch Hymenophyllaceæ are primitive, both types of stele are derivable from the Botryopterideæ. Further, Mr. Tansley has pointed out how the Hymenophyllaceous petiolar bundle, which may be from the first an open C, or may be given off

as a closed ring, is in both varieties comparable to Botryopteridean traces (32). The dimorphism of the fronds of most Botryopterideæ, and the fact that these fronds show no indications of dichotomy are points in which the fossil order seems to be less primitive than the recent. These differences, coupled with the much slighter structure of the sporangia, and the position of the annulus, would seem to the writer to forbid the derivation of the Hymenophyllaceæ from the Botryopterideæ, but the similarities between the two orders warrant the supposition that both were derived from the group of simple monostelic Palæozoic Ferns, at present ill-defined, to which Mr. Arber has given the name of Primofilices (1); the Botryopterideæ would be an important but specialized order of the group, while the Hymenophyllaceæ are probably descended from less specialized forms (24).

SCHIZÆACEÆ.

Though the course of evolution of the stele in the Schizæaceæ is still very variously interpreted, it seems to be generally agreed that the stele of *Lygodium* is the most primitive in the order. It is a protostele, and the first-formed elements are indeterminate, but show a tendency to assume a peripheral position. In *Schizæa digitata* the rhizome contains a woody ring enclosing a pith; in *S. dichotoma* and *S. malaccana* endodermal pockets are developed in connection with some of the leaf-gaps; as in *Lygodium* the protoxylem is scattered (4). Besides the endodermal pockets, Mr. Boodle records the occasional occurrence, in *Schizæa digitata*, of an isolated inner endodermis and local patches of internal tracheides, connected with or free from those of the woody ring (6). *S. malaccana* sometimes, though rarely, also possesses an internal strand, or still more rarely two such strands in its pith. But far more often the central parenchyma also contains an internal endodermis; this endodermis may be a mere rod of cells or it may enclose one or more cells (35). *Aneimia mexicana* and a few other species are truly solenostelic, while *A. Phyllitidis* and *Mohria* are dictyostelic, the meristemes being concentric and containing internal and external phloem (3).

It seems clear from Dr. Jeffrey's and Mr. Gwynne-Vaughan's researches on the ontogeny of the Ferns that the solenostele was derived from the protostele (20), (16). This conclusion is now widely accepted for the majority of ferns (33), (13). The same writers have shown that the dictyostelic type of stem usually arises from a

solenostele by the over-lapping of successive gaps left in the latter by the departing leaf-traces. There seems no reason to doubt that the dictyostely of *Aneimia Phyllitidis* and *Mohria* was evolved in this way from solenostely. As regards the phylogeny of the *Schizæa*-stele it is difficult to speak with any certainty. Mr. Tansley and Miss Chick contend that as the protostele of *Lygodium* appears to be primitive among the Ferns, it is natural to suppose that "... in *Schizæa* the central tracheides of such a stele are normally replaced by parenchyma, just as is the case in most species of *Lepidodendron*, whose structure is known" (35). They point out that such a change might result from an increase in the size of the stele, or a decrease in the demand for water-conduction. They contend that this view is supported by the small size and shade-loving habit of *Schizæa*; but they admit that the greatest objection to the view that the stele of *Schizæa* represents an advance on protostely, and is not a reduced siphonostele, lies in the difficulty of seeing a use in these internal endodermal structures in their present condition. They argue that this objection may be partly met by the suggestion that if the demand for water-conduction were lessened, this should affect the vascular tissue. They maintain that the proportion of intra-stelar parenchyma present in *Schizæa*, where there is no internal endodermis, considerably exceeds the proportion ordinarily found in fern-steles, and that such a central parenchyma will tend to become functionless for conducting purposes. They continue: "The mass of intra-stelar parenchyma is greatest at the point of departure of a leaf-trace, and here, consequently, we get the beginnings of its replacement by a physiologically extra-stelar tissue, which is definitely non-conducting" (35). This tissue is the internal endodermis and the endodermal pockets. Mr. Tansley and Miss Chick contend that so long as the stele does not increase in size the physiologically extra-stelar tissue produced within the stele remains, as in *Schizæa*, small in amount and inconstant in occurrence. They admit that their view is not the only tenable one, and suggest the alternative that the stele of *Schizæa* has been reduced from a siphonostele, and that the occasional internal endodermis is vestigial. They claim, however, that no traces of internal phloem, indicating reduction from a solenostele, have been found in a considerable amount of material, and that the ectophloic siphonostele is rare in ferns. They argue that the tracheides occasionally present in the central parenchyma would be hard to understand if *Schizæa* were reduced from an ectophloic siphonostele, and that in that case we

should expect the remains of internal endodermis to be always near the xylem ring. Against this it may be urged that an obsolescent and functionless structure might well tend to be irregular in position; but it must be admitted that it is difficult to account for the internal tracheides if the ancestors of *Schizæa malaccana* possessed a complete internal endodermis shutting off the pith from the vascular tissues.

Mr. Boodle also holds that endodermal pockets are not necessarily vestigial, and that they might arise for mechanical reasons. But he regards them as vestigial in *Schizæa dichotoma*, examined by him, because he thinks it hard to explain the utility of the isolated endodermis. He admits that the impossibility of discovering a function in any structure is an inconclusive reason for regarding that structure as vestigial, but maintains that the supposition of its being functionless is supported by its haphazard occurrence. He proceeds to compare *Schizæa* with *Aneimia*. *A. mexicana* is solenostelic; its external and internal endodermes are continuous through the leaf-gaps, while the smaller *A. coriacea*, closely resembling *A. mexicana*, also has an internal endodermis, but the endodermal pockets are independent of the latter. Mr. Boodle naturally concludes that these pockets of *A. coriacea* are the reduced remains of previous connections between outer and inner endodermes. As both these features occur locally in *Schizæa dichotoma*, Mr. Boodle considers that this suggests the view that outer and inner endodermes were once, in the phylogeny, continuous through the leaf-gaps, and that the stele of *Schizæa* is therefore a reduced ectophloic siphonostele; for he points out that there is no reason to suppose that the ancestors of *Schizæa* ever possessed internal phloem (6). Dr. Jeffrey, nevertheless, regards the stele of *Schizæa* as probably "derived by reduction from that which is characteristic of *Mohria* and *Aneimia*" (20). This view is based on an analogy with certain conclusions drawn from Dr. Jeffrey's study of the Osmundaceæ. Though there is a good deal to be said in favour of these conclusions, they are not generally accepted even for the Osmundaceæ, and there seems little reason to apply the analogy to *Schizæa*; for though the presence of vestigial internal phloem would not necessarily indicate reduction from the dictyostelic type of *Mohria* rather than from solenostely, yet its absence in *Schizæa* is a strong argument against reduction from either of these types.

To recapitulate: It seems to be generally agreed that the

protostele of *Lygodium* is primitive in the order; that the solenostelic forms were derived in the course of phylogeny from such a type; and that the dictyostelic forms arose from solenostelic types by the over-lapping of the leaf-gaps. As regards *Schizæa* we are unable on present evidence to decide whether its stele represents a progressive development from that of *Lygodium* or has been reduced from an ectophloic siphonostele. The third view, namely that the stele of *Schizæa* has been reduced from a solenostelic or dictyostelic type, may be dismissed as improbable.

The gametophyte of Schizæaceæ is generally a flat thallus (11), but filamentous prothalli have been reported from *Schizæa bifida* and *S. pusilla* (10), (38). Mr. Thomas regards the filamentous prothalli as primitive, arguing that we can hardly suppose that their structure is due to moisture, since Fern prothalli generally are only able to grow under moist conditions (38). Mr. Boodle's and Dr. Jeffrey's view that the stele of *Schizæa* is reduced, and Mr. Tansley's and Miss Chick's that the conducting tissue has decreased, are all compatible with the view that the ancestors of *Schizæa* lived under exceptionally moist conditions. But it is not necessary to assume that if reduction to a filamentous prothallus has taken place it is necessarily correlated with a damp habitat; for if *Schizæa bifida* is reduced, so is *S. pusilla*, and Mrs. Britten and Miss Taylor found a fungus in symbiotic association with the prothallus of this species (10). It should be remembered that symbiosis is a condition occurring in one of the Hymenophyllaceæ possessing a filamentous prothallus, and that it is generally held to be one of the factors that cause reduction. The view that it has done so in the case of *S. pusilla* is supported by the simple, probably reduced leaves of this species. No fungus has been found in symbiotic association with *S. bifida*, but there seems to be at least a possibility that its filamentous prothallus, if not due to a moist habitat, may have been inherited from a reduced symbiotic ancestor. Another of Mr. Thomas' arguments is that if the retention of small cellular expansions, sometimes quoted as evidence for reduction from more normal forms, is necessary for the nutrition of *Trichomanes*, it is hard to see why they are absent from *Schizæa*. But such small expansions were described by Mrs. Britton and Miss Taylor in *S. pusilla* the year before Mr. Thomas' paper was published, and they may well have been lost in the hypothetically more reduced *S. bifida*. Mr. Thomas makes use of another argument open to serious objections. He says: "That the Ferns . . . have been descended from an

aquatic ancestor is, of course, rendered probable by the character of the ciliate spermatozoids. But a specially interesting feature in *Schizæa* is the mode of development of both kinds of sexual organs as morphological equivalents of the ordinary branches of a filamentous prothallium, a mode which explains the character of these organs. Are we not, therefore, justified in regarding *Schizæa* as a primitive form? ” (36). If by morphological equivalents are to be understood homologous members, the above quotation would mean that the archegonia and antheridia of *Schizæa* were once, in their phylogeny, branches. Otherwise the words are merely a fanciful description in scientific language. But if archegonia are homologous with any more primitive structure, it is with oogonia, organs found in various positions. Even if we accept the primitiveness of *Schizæa* among vascular plants, it is presumably less primitive than the cellular Cryptogams from which it would then have arisen; but in many of these well-differentiated gametangia occur. Surely it is time to recognize that the gametangium is probably an organ *sui generis* and not a transformation of another organ, or at least to admit that a peculiar mode of development of the gametangia in a recent fern is not a proof of such extreme primitiveness as claimed by Mr. Thomas and that the homology of the gametangium is not to be decided by its mode of development in a relatively highly differentiated and vascular plant. It is only fair to add that Mr. Thomas states that the question cannot be decided on evidence from a single form, “but must rest on a broad basis of comparison of the development in the different families of Ferns” (38). He contends, however, that the occurrence of a filamentous prothallus in the Hymenophyllaceæ and Schizæaceæ and the frequency of a filamentous form in the earlier stages of development, and the tendency to become filamentous when nutrition is inadequate favour the view of the relative primitiveness of the filamentous prothallus. But if being widely spread is a sign of primitiveness the thalloid prothallus would be the primitive one, for it is far more widely spread among the Ferns. The tendency to become filamentous when nutrition is inadequate is surely a weighty argument in favour of this condition being due to reduction. The frequent occurrence of a filamentous stage in the early phases of development certainly favours the primitiveness of this condition, but it can hardly be held to weigh against so many and such strong indications that the filamentous type is reduced.

We may now compare the Schizæaceæ with the Botryopterideæ.

The simpler forms of both orders are protostelic; in the Schizæaceæ these simpler forms are exarch and the present writer holds that the Botryopterideæ were also primitively exarch, but this is doubtful and denied by many. But though the simpler types of both orders are not very different anatomically, it seems unlikely that the dichotomous fronds of some of the Schizæaceæ should have been derived from the pinnate ones of the Botryopterideæ. Potonié has laid great stress on the primitiveness of dichotomy in Fern-fronds and its prevalence in the fern-like fronds of the Palæozoic rocks (21), and his views have met with very general acceptance (18), (30). Moreover, although the Schizæaceous annulus may be two cells broad, it is not easy to derive it from the annulus of any annulate Botryopterideæ, though of course it might have originated from one of the exannulate members of the order. Thus it is unlikely that the Schizæaceæ are directly descended from the Botryopterideæ, but they may have arisen from simpler allies of the latter, from some of the Primofilices of Mr. Arber. Like the Hymenophyllaceæ, the simpler Schizæaceæ are protostelic; this probably indicates a low stage in the evolution of the stele rather than a particularly close relationship between the two orders. As it was concluded that the Hymenophyllaceæ were a series of reduction, we shall not be astonished to find that the least reduced Hymenophyllaceæ, such as *Trichomanes scandens*, are most like the simpler Schizæaceæ, such as *Lygodium*. A striking point of similarity is the occurrence of filamentous prothalli in members of both orders. This probably does not indicate close affinity, for the filamentous prothalli would appear to be secondary in both orders. The structure and origin of their sporangia is, however, essentially similar, though their distribution is different. According to Professor Bower's researches the annulus is probably homologous in the two orders (7). These characters hardly warrant the assertion of a very close affinity, but they suggest that both orders originated from allied groups of the Palæozoic Primofilices.

GLEICHENIACEÆ.

The Gleicheniaceæ are always protostelic, except the solenostelic *Gleichenia pectinata*, and *Platyzoma*, which possesses an ectophloic siphonostele. There is of course a strong presumption that the protostelic condition is primitive and that the solenostele was derived from it. In connection with the insertion of the leaf-trace, a "nodal island" is found in most of the protostelic Gleichenias.

These "nodal islands," consisting of pouches of phloem enclosed in the stele and, sometimes containing an endodermis, extend downwards into the internode for a varying distance. Mr. Boodle first and Mr. Tansley later have pointed out that the solenostele of *G. pectinata* probably arose by the continuation downwards through the internode of an unusually bulky nodal island and its junction with the one developed in connection with the node below (5), (33). Mr. Boodle points out that the nodal island might be regarded as evidence that the protostele has been reduced from a solenostele, but that the fact that the young stem is at first protostelic renders this improbable. Further the dichotomy of the fronds of many Gleicheniaceæ renders it quite likely that the order is a relatively primitive one. In the xerophytic *Platyzoma* the departing leaf-traces, which are very small and much crowded, leave no gap in the stele. Its xerophily and the smallness of its leaves make it very probable that it has arisen from a solenostelic form by reduction. This view is held both by Mr. Tansley and by Mr. Boodle (5), (33).

Concerning the form of the leaf there seems no reason to doubt the view that, as is usually the case, the dichotomous fronds of most species of *Gleichenia* are more primitive than the simple pinnately lobed leaves of *G. moniliforme* and *G. simplex*, both of which appear to be somewhat reduced. *Platyzoma* has truly pinnate leaves, but this seems to be a secondary modification, a case of forking mentioned by Professor Bower favouring this view (7).

In comparing the Gleicheniaceæ with the Botryopterideæ we find in the simpler members of both orders a solid protostelic cylinder. In the Gleicheniaceæ the protostele is always mesarch; but the amount of centrifugal xylem present varies in different species, and, on the view advanced here, such a species as *G. vestita*, in which the protoxylem is relatively deeply seated, has diverged further than most species from the hypothetically exarch and protostelic ancestor of Botryopterideæ and Gleicheniaceæ. The dichotomy of most Gleicheniaceous fronds seems to show that they are more primitive than any Botryopteridean fronds known to us. Moreover the sporangia of the Gleicheniaceæ differ so widely from those of the Botryopterideæ as to forbid our deriving the former from the latter order. For example it is impossible to regard the annulus of the Gleicheniaceæ as homologous with that of the annulate Botryopterideæ; both types of annulus must have arisen independently from an exannulate sporangium. It then appears that the Gleicheniaceæ and Botryopterideæ have in common

certain probably primitive characters, but that those characters that are especially Botryopteridean are not found in the Gleicheniaceæ. Presumably therefore the latter arose from Primoflicies allied to, but less specialized than the Botryopterideæ.

Protostely occurs both in Gleicheniaceæ and Hymenophyllaceæ and the writer believes that it is primitive in both cases. It is only the larger Hymenophyllaceæ that resemble the Gleicheniaceæ, and this is what we should expect if the filmy character of the fronds indicates reduction. But the simplest Gleicheniaceæ appear to have diverged further than *Trichomanes scandens* from the exarch protostele which the writer regards as primitive, for their xylem is mesarch. Again, though the fronds of the more primitive members of both orders are dichotomous, those of the Gleicheniaceæ are less primitive, inasmuch, as the angle of the dichotomy is occupied by a bud. Professor Bower has shown that the relative proportion that the two faces into which the oblique annulus of the Gleicheniaceæ divides the sporangium bear to one another varies considerably within the order and that every gradation between the two extremes is met with (7). This would make it probable, as Professor Bower claims, that the annulus is homologous throughout the annulate Leptosporangiatæ (8). This probable homology of the annulus and the similar leptosporangiate origin of the sporangia suggest a certain, though a very remote relationship for the two orders.

To the Schizæaceæ the Gleicheniaceæ seem to bear a closer relationship than to the other orders hitherto discussed. The protosteles of the more primitive members of each order differ, it is true, in the position of the protoxylem; in this the mesarch Gleicheniaceæ are, on the view advanced here, less primitive. But the dichotomy of the frond of *Gleichenia*, in which genus a bud is formed in the angle of the dichotomy, is exactly paralleled in the more primitive Schizæaceæ, and such branching of the frond is a rare feature. Professor Bower is of opinion that the cell or cells enclosed by the sub-apical annulus of the Schizæaceæ correspond to the face of the Gleicheniaceous sporangium that is directed obliquely away from the sorus. This face of the sporangium may in the Schizæaceæ be reduced to a single cell, but the view of the homology of the annulus in the two orders is strongly supported by the variation of the relative size of the two faces of the sporangium within the genus *Gleichenia*. Such a theory is not, of course, tenable if we accept Potonié's view that the Schizæaceous

annulus made its first appearance as a group of apical cells. This view was largely based on the apparently Schizæaceous affinities of the Upper Carboniferous *Senftenbergia* where the annulus appears to be an apical cap of cells, not a ring enclosing one or more cells. But recent discoveries have thrown doubt on the filicinean character of many of these fern-like fructifications, and it is therefore not impossible that *Senftenbergia* (which, however, resembles the Schizæaceæ, in that its sporangia are non-soral) is the male organ of a Pteridosperm. But even if the annulus is homologous in the two orders there remains the important difference that the Gleicheniaceæ are soral and the Schizæaceæ non-soral. In view of the striking similarities of the vegetative organs of both orders we are driven to one of two alternatives: either that in the Schizæaceæ the sporangia represent reduced monangic sori, or that fresh sporangia have been developed in the evolution of the Gleicheniaceæ sorus, either by septation of a single sporangium or by interpolation of fresh sporangia. Since the monangic condition is exceptional in the Ferns it is probable that the single sporangia of the Schizæaceæ represent reduced sori. But it should not be forgotten that Professor Bower has shown that there is every probability that in the evolution of *Gleichenia dichotoma* an interpolation of supernumerary sporangia has occurred. Thus the similarities between the two orders are sufficient to indicate that the common stock from which they are derived lies considerably less far back than do the common ancestors of Gleicheniaceæ and Botryopterideæ or of Gleicheniaceæ and the filmy Ferns.

MATONINEÆ.

Matonia, the only genus of the Matonineæ, shows a considerable range of anatomical complexity. Its stem may possess two concentric solenosteles of which the inner encloses only a pith (37), or the inner solenostele may contain in the centre of the pith a strand of xylem, while in other cases this central strand is itself converted into a third solenostele (39). The evolution of polycyclic solenostely has recently been so fully traced in this journal that it would be superfluous to do more than briefly to recapitulate the explanation given. It has been shown conclusively that the internal solenosteles arise in the ontogeny as a local thickening of the edge of the gap left by the departing leaf-trace in the stele immediately outside it; the strand thus formed, as it increases in size,

assumes a central position in the internode; but at the node it connects again with the stele from which it originated. As this strand increases in size, phloem, endodermis and parenchyma appear in it, and, after it has thus attained to solenostely, another stele arises in the same way as a local thickening of the gap formed in this second solenostele by the departure of the strand that fuses with the original external stele when the latter gives off a leaf-trace. There can be very little doubt that polycyclic solenostely originated in the phylogeny in the same way as in the ontogeny, and that one of the ancestors of *Matonia* must have contained a single solenostele. Unfortunately, although we are acquainted with a certain number of Mesozoic fossils, such as *Laccopteris* and *Matonidium*, which are referred with some certainty to the Matonineæ on account of the branching of their fronds, they are preserved only as impressions and we know nothing of their anatomy (27).

There is little in common between the Matonineæ and either Botryopterideæ or Schizæaceæ. Such similarities as the origin of the sporangia and the modified dichotomy of the frond, in which the Matonineæ resembles the two other orders, appear to indicate a remote common origin rather than a close affinity.

It is to the Gleicheniaceæ that the Matonineæ show the closest affinity. It has been shown that the ancestors of *Matonia* must have passed through a solenostelic stage in which their stele resembled that of *Gleichenia pectinata*. Dr. Scott has shown that the acquisition of centrifugal xylem, advantageous because its development is unlimited, frequently causes the reduction and eventually the suppression of the centripetal wood or its conversion into pith (25). The centrifugal wood was presumably acquired early in the Gleicheniaceous cycle of affinity, since the protostelic species of *Gleichenia* are mesarch. It is not, however, contended that *Matonia* arose from a solenostelic *Gleichenia*, for solenostely, being only known in one exceptionally large species, appears to have arisen comparatively recently in the Gleicheniaceæ. What is suggested is that the polycyclic solenostely of *Matonia* was evolved from simple or monocyclic solenostely; that this single presumably endarch solenostele may well have arisen from a mesarch solenostele or protostele by the abortion of the centripetal-xylem or its replacement by pith. Such a solid mesarch protostele would be distinctly Gleicheniaceous in its affinities. Such an origin would not be incompatible with the development of the frond as explained

by Mr. Tansley and Miss Lulham (37). They point out that the primary division of the frond is a dichotomy in the angle of which a middle pinna is developed; and that the young plant shows a tendency to produce fronds that branch dichotomously. They suggest that the peculiar fan-like adult frond of *Matonia* arises "by dichotomy of the primary forks and the repeated dichotomy of the *lower member only* of each successive fork, the upper member in each case and the lower also of the last fork, becoming a pinna" (37). They point out that on this view the two main recurved branches of the frond are sympodial structures composed of the bases of lower members of successive dichotomies, and that this is suggested by their scorpioid form. Further, the hypothesis that this type of frond is a modification of a dichotomous one enables us, as the same writers remark, to bring *Matonia* into relation with *Gleichenia*, several species of which show a tendency for the lower members of the dichotomy to divide again, while the upper ones form pinnae. The middle pinna of *Matonia*, whatever its origin, may be compared with the bud occupying the axil of the dichotomy of the fronds of *Gleichenia*. Thus there seems good reason for supposing that *Matonia* may have originated from the simplest *Gleicheniaceæ*, or from forms very close to them. Anatomically *Matonia* is much more complex, but if the anatomy of the Mesozoic *Matonineæ* were known they might serve to bridge this gap.

CYATHEACEÆ AND POLYPODIACEÆ.

The Cyatheaceæ and Polypodiaceæ are clearly closely related and it is convenient to discuss their anatomy at the same time. Probably the most primitive type of stele found in either order is that known as the *Lindsaya*-type. Its structure is practically that of a protostele, but embedded in the dorsal part of the xylem is a strand of phloem. Mr. Tansley and Miss Lulham point out that the "nodal islands" of *Gleichenia* indicate the manner in which the more bulky phloem strand of *Lindsaya* may have arisen (36). Indeed we can see that if a nodal island were to become somewhat larger, to consist only of phloem and to be continued through the internode until it met another nodal island we should have a structure closely similar to the *Lindsaya*-stele. It has been shown that nodal islands are formed in connection with leaf-gaps; this is presumably phylogenetically true of the *Lindsaya* phloem-strand, and explains the position of the latter near the dorsal surface of the rhizome. This *Lindsaya*-type occurs in several Polypodiaceous

genera. Mr. Tansley and Miss Lulham have traced the evolution of solenostely from it by the decurrency into the internode of the phloem-strand (in which, as it increases in size, endodermis and pith are developed) and by its junction with the similar strand developed in connection with the leaf-trace of the node below (36). All the phases of this process have been found in the Cyatheaceæ or Polypodiaceæ. It appears that the first tissue to appear within the stele of these orders when protostely was departed from was in every case phloem. The great majority of the Cyatheaceæ and Polypodiaceæ, even the complex polycyclic dictyostelic forms, pass through an ontogenetic phase in which their xylem, like that of *Lindsaya*, contains only a strand of phloem. Mr. Chandler examined a large number of young ferns of these orders and came to the conclusion that those cases in which other tissues appeared within the xylem before internal phloem were due to "short-cuts" of evolution and that the parenchymatous cells in the centre of the stele were best regarded as potential phloem (13). On the other hand certain species of *Vittaria* and *Antrophyum* possess little or no internal phloem even when mature (17), (20). This is clearly due, as Dr. Jeffrey first asserted, to reduction (20).

A considerable number of ferns have retained a solenostelic structure. Mr. Gwynne-Vaughan has shown that two types of dictyostely have been evolved from it by the overlapping of leaf-gaps. In the dorsiventral forms the leaves are inserted in two rows, and when the gaps left in the stele by the departure of their traces overlap, the dorsal part of the solenostele becomes a small dorsal strand, while the ventral part from which no leaf-traces are given off remains unreduced. In transverse section this type usually shows a large gutter-shaped stele open dorsally, and in the dorsal gap a much smaller stele; but if the leaves are inserted nearly opposite one another on the sides of the rhizome the dorsal and ventral steles are more or less of the same size. In the radial dictyostelic forms the leaves are inserted all round the stem so that the gaps left by them are constantly changing, and the vascular strands therefore continually anastomosing. Mr. Gwynne-Vaughan's work proves that dictyostely (so-called polystely) arises not by branching, but, as Dr. Jeffrey first contended (20), by the overlapping of the leaf-gaps. Miss Ford, however, describes the stele of *Ceratopteris thalictroides* as dividing directly into two (15), and Mr. Chandler describes how the stele of *Polypodium aureum* appears to break directly into two and later into more numerous strands (13).

The former suggests that *Ceratopteris* has followed a different course of evolution from other dictyostelic ferns (15), but Mr. Chandler regards the splitting of the cauline strand "merely as an anticipation of the characteristic double nature of the leaf-traces" (13). He points out that in the complex forms the leaf-trace usually originates from two separate strands and that a splitting of the cauline strand to give rise to these strands from which the trace originates is the most obvious preparation for the departure of the latter (13). This view, bringing *Polypodium aureum* and *Ceratopteris* into line with other dictyostelic Ferns, is more satisfactory than Miss Ford's. *Ceratopteris* has undergone reduction, probably owing to its aquatic habit, and this may account for the suppression in its ontogeny of some of the stages hypothecated in its phylogeny. In some cases the solenostele seems to have become dictyostelic by the formation of gaps, generally in the ventral part of the stele, unconnected with the departure of the traces (17). For these gaps Mr. Tansley has suggested the name "perforations" (34).

Polycyclus also occurs in the orders under consideration. In its development it resembles the polycyclus of *Matonia* (*q.v.*) and every stage in its evolution from the thickening of the edges of the leaf-gap in a solenostele to a tetracyclic condition has been recorded within the two orders.

The fronds of the orders are usually pinnately divided; but Mr. Seward and Miss Dale have shown that in *Dipteris* the frond is dichotomous. That this is a primitive character is borne out by the presence of *Dipteris*-like fronds from the rocks ranging from the Triassic to the Cretaceous (28).

Professor Bower has shown that whereas in all Cyatheaceæ, and some Polypodiaceæ, the sporangia arise in basipetal succession on a receptacle, in other Polypodiaceæ they develop without any definite order, forming a "mixed sorus" (7). Miss Armour has recently shown that in some species of *Dipteris* the sporangia originate simultaneously, while in other species the sorus is of the mixed type (3). Professor Bower has shown that the sorus in which the sporangia originate simultaneously is the most primitive, that the sorus showing basipetal succession of the sporangia originated from this type and itself gave rise, in several series of forms, to a "mixed sorus." Another point brought out by him is that the oblique annulus, retained by most Cyatheaceæ, has become vertical and incomplete in most Polypodiaceæ (7). In a few, notably in *Dipteris*, the annulus is somewhat oblique and the geological

record of that genus certainly bears out Professor Bower's view that this obliquity is primitive.

The Cyatheaceæ and Polypodiaceæ do not appear to approach the Botryopteridæ at all closely, but we shall see later that there may possibly be a connection through the Gleicheniaceæ between the Cyatheaceæ and Polypodiaceæ and certain Primofilicinean ancestors of the Botryopteridæ.

To the Hymenophyllaceæ, the Cyatheaceæ and Polypodiaceæ show hardly any points of resemblance, except those characteristic of the Ferns generally. The basipetal succession of the sporangia in the filmy ferns, and some Cyatheaceæ and Polypodiaceæ, is probably due to parallel development. It is fair to add that Diels suggests a rather close affinity between the Hymenophyllaceæ and Polypodiaceæ, but he adduces no fresh evidence in support of this idea (14). While we cannot look upon the Schizæaceæ as the ancestors of the Cyatheaceæ and Polypodiaceæ we may expect a close affinity to the Gleicheniaceæ.

Some structure resembling the "nodal island" of *Gleichenia* was probably the precursor of the dorsal phloem-strand of the *Lindsaya*-stele. The C-shaped trace of the Gleicheniaceæ is frequently found in the anatomically simpler Cyatheaceæ and Polypodiaceæ, while the numerous varieties of traces in the more complex forms are all referable to more or less profound modifications of this original C-shaped type. Though the fronds of the Cyatheaceæ and Polypodiaceæ are usually pinnately divided, the relatively ancient genus *Dipteris* has retained a form of dichotomy. Further, the sporangia of all three orders are soral. In *Gleichenia* the sporangia usually form a single series (as do those of some species of *Dipteris*), but in *G. dichotoma* there are supernumerary sporangia (7) and these, though they arise simultaneously with the others, foreshadow the elongation of the receptacle on which the sporangia of the Cyatheaceæ and simpler Polypodiaceæ occur in basipetal succession. Professor Bower has also established the homology of the annulus in these orders (7). On the whole, then, the similarities enumerated above seem to indicate that it is among the most primitive Gleicheniaceæ, now extinct, that we must look for the ancestors of the Polypodiaceæ and Tree Ferns. But since the stele of *Loxsonia* is exarch and since this genus, from its similarity to these orders, presumably had a relatively recent common origin with them, and since its exarchy appears, on general grounds, to be primitive, it is likely that the Gleicheniaceous ancestor of the Cyatheaceæ and

Polypodiaceæ had not acquired any centrifugal xylem. In the great majority of cases the xylem of the two latter orders is endarch, and the centripetal wood has been completely replaced by pith, but *Dipteris*, which has been shown to be relatively primitive in many ways, retains a certain amount of centripetal wood. The origin of the Cyatheaceæ and Polypodiaceæ from the Gleicheniaceæ was suggested as early as 1895 by Dr. Campbell (11).

Some botanists have regarded *Matonia* as intermediate between the Gleicheniaceæ and Cyatheaceæ, and it has even been included in the latter order. Later researches have established its affinity with the Gleicheniaceæ, but if the Cyatheaceæ originated from the simplest Gleicheniaceæ a common origin for *Matonia* and the Tree Ferns at a relatively not very remote period is assured. The occurrence of the *Lindsaya*-type in the Polypodiaceæ, and the close affinity between this order and the Cyatheaceæ prove that their solenostely—even when monocyclic—originated independently of the solenostely of *Matonia*. Professor Bower includes the Gleicheniaceæ-*Matonia*-*Dipteris* series among the few probable lines of phyletic origin traced by him. However he does not seem to contemplate the origin of *Dipteris* from *Matonia*, for he admits that, though their vascular systems are of the same type, that of *Matonia* is more complex. Nevertheless, after discussing the sporangia of *Dipteris* and concluding that they resemble those of the Cyatheaceæ, he claims that the incomplete annulus “points to a further departure from the primitive type such as may with reasonable probability be found in the sporangia of *Matonia* and ultimately of *Gleichenia*” (9). He adds that the anatomy bears out this comparison. His researches certainly show that a sorus in which the sporangia develop basipetally or without definite succession is derived from a sorus in which they originated simultaneously. But though in species of *Dipteris* the sporangia of a sorus may originate simultaneously, there is no reason to construct a phyletic line passing through the more complex *Matonia* to *Dipteris*, for Professor Bower has shown that these changes in the construction of the sorus have taken place in more than one evolutionary series. *Dipteris* is more primitive than *Matonia*, not only in the absence of any indication of polycyclus, but in its mesarchy and in the branching of its frond, which appears less specialized than the peculiar branching of the frond of *Matonia*. And lest it should be thought that *Dipteris* might have originated from [simpler extinct Matonineæ, we must bear in mind that though these may have possessed a mesarch

solenostele, yet we know from the fossil record that the type of branching of the fronds of *Matonia* was characteristic of its Jurassic allies. It seems not unlikely that the solenostele of *Dipteris* originated with the Polypodiaceæ, the order in which the genus is usually included, but if in accordance with Mr. Seward and Miss Dale, supported by Professor Bower, we make *Dipteris* into a separate order, the Dipteridineæ, the near allies of this order would seem to be the simpler Polypodiaceæ and the Gleicheniaceæ, and not as Professor Bower suggests the Matonineæ. To the Polypodiaceæ *Dipteris* shows its affinity in its anatomy, while it approaches *Gleichenia* in the dichotomy of its frond (although the axillary bud of the latter genus is not represented in *Dipteris*) and in its mesarchy. The solenostele of *Gleichenia pectinata* appears however to be a recent development of the genus and to have originated independently of that of *Dipteris*.

As regards the relationship of the Cyatheaceæ to the Polypodiaceæ it is impossible to doubt their close affinity. The vertical annulus found in most Polypodiaceæ seems to be less primitive than the oblique annulus of the Tree Ferns; the regular basipetal succession of sporangia on the receptacle also appears to have been lost by some Polypodiaceæ. On the other hand the tree-like habit of the Cyatheaceæ appears to be a recently acquired character.

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THE BRITISH VEGETATION COMMITTEE'S EXCURSION TO THE WEST OF IRELAND.

THE excursion of the Central Committee for the Survey and Study of British Vegetation, organised and conducted by Mr. R. Lloyd Praeger, and lasting from August 27th to September 1st, was by far the largest and longest yet attempted. It was attended by seven members, F. J. Lewis, C. E. Moss, R. Lloyd Praeger, A. G. Tansley, F. E. Weiss, T. W. Woodhead and R. H. Yapp, and by four visitors, Mr. Adamson, Professor F. O. Bower, Mr. F. T. Brooks and Professor W. E. Praeger (Kalamazoo, Michigan). The members were greatly indebted to their leader, whose admirable arrangements and knowledge of the country and its botany enabled the party to spend the available time to the best advantage.

The two areas investigated were the low-lying bogs and some of the hills of Connemara (County Galway), and the carboniferous limestone region on the borders of Galway and Clare.

CONNEMARA.

Connemara is a country of barren hills of metamorphic rock enclosing great stretches of nearly flat bogland, not many feet above sea level, interspersed with innumerable lakelets. The party spent a long day in the southern part of the most extensive area of this

type of country, that lying between Roundstone and Clifden, and bounded on the south by the hill Errisbeg and the coast, and on the north-west by the mountain mass known as "the Twelve Pins" (or Beinns). An afternoon was devoted to the dunes of the coast, and a morning to the ascent of the southernmost "Pin," Ben Lettery.

Submerged Aquatic Vegetation.

The peaty waters of the loughs contain *Lobelia Dortmanna*, *Subularia aquatica*, *Isoëtes lacustris* and *Pilularia globulifera*, among completely submerged plants, as well as *Potamogeton natans* and *Eriocaulon septangulare*, which is also abundant in shallow roadside pools. These plants grow in very open association towards the gravelly margins of the loughs, under two to eight feet of water. *Eriocaulon* and *Lobelia* in sheltered inlets reached a length of three feet. One of the loughs near the sea, south-west of Roundstone, holds *Naias flexilis*, but the height of the water made it impossible to obtain specimens.

Reed-swamp Vegetation.

The margins of a few of the loughs showed a narrow reed-swamp of *Phragmites communis* and *Cladium Mariscus*, but this association was poorly represented in the area. There were, however, here and there small tracts of bog in which *Cladium* and *Phragmites* were abundant, no doubt representing the sites of small lakes obliterated by vegetation.

Flat Bog or "Flachmoor" Type.

The bog itself, of the type known to the Germans as "Flachmoor," was in the wetter parts dominated by *Rhynchospora alba*¹; *R. fusca* also occurs, but is rare and isolated. *Schæenus nigricans* was sub-dominant in this type of bog, species of *Sphagnum* were locally sub-dominant, while *Drosera rotundifolia*, *D. anglica*, and *D. intermedia*, *Myrica Gale*, *Narthecium ossifragum*, *Menyanthes trifoliata*, *Erica Tetralix*, *Eriophorum vaginatum* and *E. angustifolium*, with the *Cladium* and *Phragmites* already referred to, were freely associated, *Calluna* occurred quite locally in the bog. Hummocks of *Racomitrium* and *Leucobryum*, with *Sphagnum* ("Hochmoor"-type) occurred in places.

A slightly drier type of bog was dominated by *Molinia caerulea* var. *depauperata*, forming characteristic tussocks. This variety is much smaller than the type and has only one spikelet to each branch of the inflorescence. The other elements of this kind of bog (which is more extensive than the *Rhynchospora*-type) included more of the heaths (*Calluna* and *E. Tetralix*), though these still occurred only as isolated plants. This drier type of bog shades off into the *Rhynchospora*-type and apparently represents a further stage in land-formation. Round the lake of Craigga Moor, *Erica Tetralix*

¹ The "Flachmoor" of the Sihlthal near Einsiedeln, Switzerland, visited by one of the party in July, was similarly partly dominated by this species, with many of the same associates.

was largely replaced by the rare *E. Mackaii*, but no trace could be found of *E. Stuarti*, a supposed hybrid between the latter and *E. mediterranea*, and perhaps exterminated by the discoverers, nor of the double-flowered variety of *E. Mackaii*, named by gardeners *E. Crawfordi*. One patch containing many plants of *Erica mediterranea* was found by a streamside, but it flowers in the spring.

On the knolls of metamorphic rock *Ulex Gallii* was a conspicuous feature, associated with *Calluna vulgaris*, *Erica cinerea*, and the large-flowered *Dabeocia polifolia*, another of the rare West Irish heaths, which occurs in great profusion on all the roadsides in this district.

Errisbeg, an isolated hill only just short of 1000 feet, bears *Molinia*-bog on its northern face, while its southern steeper face is covered with a "grass-heath" association, dominated by grasses and with masses of *Ulex Gallii* in full flower. In this association were *Lastræa æmula*, *Spiranthes autumnalis*, *Scabiosa succisa* and *Plantago coronopus*. The heaths themselves were nowhere dominant on this slope.

Most of the sides of Ben Lettery (1904 feet) were covered with *Molinia*-bog. In places were patches of *Eriophorum* and *Scirpus cæspitosus*. *Blechnum boreale* was abundant and higher up was a lot of *Nardus stricta*. The last 700 feet to the summit was nearly pure *Calluna*, with *Erica cinerea* and a little *Dabeocia*. Near the top were *Empetrum*, *Arctostaphylos* and *Vaccinium Myrtillus*, with a little *Saxifraga umbrosa*, and, on the summit, *Salix herbacea*.

The moors on the borders of Wicklow and Dublin, which were visited by the Committee during the meeting of the British Association, were interesting, not only in themselves, but also because they had been mapped and described.¹ The moors cover the summits and upper slopes of the hills. The plant association covering the hill-tops was dominated by *Scirpus cæspitosus*. The soil consists of rather wet peat to a depth of several feet. The hill slopes below the *Scirpus* moor was a typical association of *Calluna vulgaris*, developed on rather drier and shallower peat. Mixed with the heather were *Vaccinium Myrtillus*, *Empetrum nigrum*, and (rarely) *Listera cordata*. This zonation of *Calluna*- and *Scirpus*-moors is of great interest, and affords a remarkable parallel to that of the Pennine peat moors, where *Calluna*-moors occupy precisely the same relative position, while *Eriophorum*-moors occur in the place of the *Scirpus*-moors.

A very interesting feature of both the *Calluna*- and *Scirpus*-moors was the occurrence in some abundance of patches of the woolly moss *Racomitrium*.

A precipitous edge was dominated by *Vaccinium Myrtillus*, with a great deal of *Pteris* in places.

The lower slopes of the hills were occupied by various types of heath pasture. The wetter places had much *Juncus*, the drier, much *Ulex Gallii* or *Pteris* or both.

WOODLAND-TYPE OF CONNEMARA.

The rocky islands in Craigga Moor Lough (and other neigh-

¹ G. H. Pethybridge, and R. Ll. Praeger. Vegetation of the District lying to the south of Dublin. Proc. Roy. Irish Acad. 1905.

bouring loughs) supported along the shores and in the tiny ravines a dense growth of dwarf trees four or five feet high, including *Quercus sessiliflora*, *Pyrus Aucuparia*, *Ilex Aquifolium*, *Taxus baccata* and *Salix aurita*, with *Calluna*, *Arctostaphylos Uva-ursi*, *Juniperus nana*, *Ulex Gallii* and *Myrica Gale*. This scrub sheltered a true woodland flora of *Primula acaulis*, *Melampyrum montanum*, *Luzula maxima*, *Hymenophyllum tunbridgensis* and *Listera cordata*.¹ This is the highest type of plant-association found in the immediate neighbourhood of the flat bogs. Its occurrence on the islands and not on the rocky shores of the loughs excited some speculation, but the problem was not satisfactorily solved.

Near the base of Ben Lettery good natural wood of the Oak-birch type was met with. *Q. sessiliflora* was dominant, and associated were *Betula*, *Pyrus Aucuparia*, *Ilex aquifolium*, and *Salix aurita*. *Aspidium Filix-mas*, *Athyrium Filix-femina*, *Oxalis acetosella*, *Melampyrum* sp., *Primula acaulis*, and *Digitalis purpurea* were among the constituents of the ground flora. Scrub of the same type also occurred in an old quarry at the base of the hill itself, and also in a gully some little distance up. It seems probable that this type of wood, dominated by *Q. sessiliflora* is characteristic of the metamorphic rocks of the west of Ireland.

The woods in the valley of Glendalough (County Wicklow) were visited by one of the party after the meeting of the British Association. They line the steep sides of the valley on the south side on non-calcareous Ordovician rocks, and the mass of them are composed of *Quercus sessiliflora* practically pure, with a little *Betula* and *Pyrus Aucuparia*, and Hazel locally. Towards the upper edge there is much Birch, Holly and Mountain Ash, passing into *Calluna*-moor with *Pteris* dominant in sheltered places. The few oaks here are much stunted and often appear half killed by exposure, which the Birch and Mountain Ash seem able to resist. Seedlings of the latter are abundant on the open moor near the wood-edge.

The ground-flora of the lower slopes of these woods are characterised by the general dominance of Mosses (species of *Dicranum*, *Hypnum*, *Polytrichum*, *Sphagnum*, etc.), indicating very wet conditions. Associated with these are many Liverworts, both thalloid and leafy. *Lastrea oreopteris* is locally dominant. *Pteris aquilina*, *Athyrium Filix-femina*, *Blechnum boreale*, *Polypodium vulgare* are abundant. Of Phanerogams *Viola palustris* is very abundant and *Pinguicula vulgaris* occurs. Besides these, *Vaccinium Myrtillus*, *Calluna vulgaris*, *Erica cinerea*, *Potentilla silvestris*, *Solidago Virgaurea* (agg.), *Lysimachia nemorum* and *Luzula maxima* occur freely. These woods extend right down the vale of Clara to the neighbourhood of Rathdrum. While clearly belonging to the *Quercus sessiliflora* type, they appear to represent a well-marked damp sub-type which also occurs in the North Welsh valleys (though there with hazel as a sub-dominant). Many of the South Wicklow woods are completely replanted with Larch.

The following diagrams give a rough idea of the seriation (and probable natural succession) of the principal plant-associations met with in Connemara during the excursion.

¹ See R. L. Praeger, *Irish Naturalist* V., p. 292, 1896.

BOG SUCCESSION.
Molinia-bog.
 |
Rhynchospora-bog.
 |
 Reed-Swamp.
 |
 Submerged aquatic
 vegetation.

ROCKY KNOLL AND HILLSIDE
 SUCCESSION.
 Oak-birch wood.
 |
 Heath-pasture and Heather-
 moor with *Ericaceæ* and
Ulex Gallii.

Some comparisons may be made between the moorlands of Connemara and similar tracts of country in the N.W. Highlands, the Hebrides and the Shetlands. In these Scottish areas *Scirpus cæspitosus* dominates the most characteristic association. In N.W. Sutherland, the flat basaltic plateau of Northern Skye, and the valley floors and gently sloping hillsides of Shetland, this type remains dominant over many hundred square miles, associated with *Eriophorum vaginatum*, stunted *Calluna*, *Erica Tetralix*, *Narthecium ossifragum*, and Sphagnum, with mounds of *Racomitrium lanuginosum* in drier places.

In the western portion of N. Uist the *Scirpus cæspitosus* association extends over hills of low elevation and broad shallow valleys, while hills in the eastern part of the island of similar altitude and character to Ben Lettery support an association dominated by *Calluna* and *Eriophorum vaginatum*. The *Rhynchospora* type of bog does not appear to be a marked feature in any of these Scottish areas. The difference in character between the surface of the moors in Connemara and districts in N.W. Scotland, such as the borders of Caithness and Sutherland north of Forsinard, is very striking. Both districts are covered with a very similar vegetation, but while the Irish area presents an almost unbroken surface, the Scottish moors are traversed by deep channels often cut eight or ten feet into the peat. On the Connemara moors peat appears to be forming rapidly at the present time, but in Shetland, Caithness and Sutherland, with many parts of the Outer Hebrides, denudation appears to be more rapid than growth. Passing farther north, peat-formation appears to have almost ceased in the west and south of Iceland, for whilst the upper layers of peat contain much *Scirpus*, the moors are now covered with two or three feet of fine dust supporting a much drier type of vegetation.

SAND-DUNES AND SHORE PLANTS.

The sand-dunes of Dog's Bay, south-west of Roundstone, were of some interest. As is so often the case in a country of hard rock they formed an isthmus connecting a rocky "island" with the mainland. The dunes themselves were largely formed of the tests of Foraminifera, and at intervals were Neolithic kitchen-middens composed of the shells of *Patella*, etc. From the physiographical and ecological standpoint, the dunes were of a degraded type, having suffered much denudation. The surface was largely bare, and bore some *Triticum junceum* but no *Psamma arenaria*, except a few little tufts remaining on the tops of some of the hummocks. The whole isthmus has evidently passed through the stage of turfy fixed

dune, and still shows this type in parts, with *Eryngium maritimum*, but there is no fresh growing dune with vigorous *Psamma*. In places the turf bore much *Asperula cynanchica* and the rare *Arabis ciliata* and *Euphrasia salisburgensis*. The existence of these "calcicole" plants (together with *Orchis pyramidalis*, *Chlora perfoliata*, etc.) not only on the dunes, but also in isolated spots away from the sea, is no doubt due to the calcareous sand which is sometimes carried some distance inland by the wind. *Arenaria peploides*, *Polygonum Raii* (a maritime segregate of *P. aviculare*) and *Spergularia rupestris*, a glandular species with characteristic pyriform seeds, were also found on the shore.

The rocky headland or "island" beyond the dunes bore a turf of *Cynosurus* and *Bromus*, with no heath-grasses. This represents a natural grass association which as yet does not appear to have been studied or described.

THE CARBONIFEROUS LIMESTONE REGION OF SOUTHERN GALWAY AND COUNTY CLARE.

Three nights were spent by the party at Ardrahan, near the borders of Galway and Clare, and a good opportunity afforded of examining this remarkable country. The region consists mainly of a nearly flat plain of limestone "pavement" with deep vertical fissures (cf. the Craven district of West Yorkshire), the whole being more or less overgrown with vegetation. From this plain rise bold hills, whose sides frequently present a regular succession of cliffs and terraces, and whose summits consist of extensive plateaus of similar "pavement." The sculpturing of these hills is often wonderfully symmetrical, owing to the horizontal position and uniform character of the successive beds of limestone.

Most of the extensive limestone plain is less than 100 feet above the sea; it is pastureland divided up into small fields by stone walls, which seem to be often put up more for the sake of getting the stones off the land than with the object of enclosure. This land bears in places a remarkable mixture of "calcicole" and "calcifuge" plants. The following were observed, mostly in the immediate neighbourhood of Ardrahan.

Of "calcicole" species were *Dryas octopetala*, locally pure in extensive sheets, *Sesleria cærulea* (sub-dominant) *Geranium sanguineum*, *Centaurea Scabiosa*, *Gentiana verna*, *Chlora perfoliata*, *Galium silvestre*, *Euphrasia salisburgensis*, *Kæleria cristata*. Other species, very characteristic of calcareous soils, though not confined to them, were *Gentiana Amarella*, *Gymnadenia conopsea*, *Carex glauca*. *Triodia decumbens* was often sub-dominant, *Briza media* and *Agrostis* sp. very abundant. Besides these were noted *Linum catharticum*, a form of *Geranium Robertianum* much like the var. *purpureum* of the English shingle beaches, *Hypericum pulchrum*, *Parnassia palustris*, *Cratægus monogyna* (gnawed down), *Potentilla fruticosa* (very local, abundant near Castle Lough), *Pimpinella Saxifraga*, *Conopodium denudatum*, *Daucus Carota*, *Scabiosa succisa*, *Antennaria dioica*, *Leontodon hispidus*, *Centaurea uigra*, *Galium verum*, *Teucrium Scorodonia*, *Plantago maritima*, *Corylus Avellana* (often forming a thick extensive scrub), *Carex pulicaris*, *Juniperus*

nana, *Pteris aquilina*, *Ceterach officinarum*, *Scolopendrium vulgare* (abundant in the limestone fissures), *Asplenium Ruta-muraria*, *A. Trichomanes*. Of markedly "calcifuge" species were *Calluna vulgaris*, *Molinia cærulea*, and *Carex binervis*. It will be seen that this is a very queer mixture of plants. The close association of plants typical of calcareous and non-calcareous soils respectively has been called a *limestone heath*.¹ These low-lying limestone pastures are also interesting as containing such a generally montane species as *Dryas octopetala*, and *Plantago maritima*, characteristic of muddy salt marshes, but also found on certain British mountains.

The plateau on the top of Slieve Carran (1,075 feet) presented the same geological formation and the same type of vegetation. Much of it was pure *Calluna*-heath with *Pteris aquilina*, the stiff erect form of *Potentilla silvestris*, *Campanula rotundifolia*, *Galium verum* and *Rubus saxatilis*. Besides these were *Alchemilla filicaulis*, *Dryas octopetala*, *Rosa spinosissima*, *Scabiosa succisa*, *Primula acaulis*, *Euphrasia salisburgensis*, in places great quantities of *Dryas octopetala*, and on the summit-cairn *Saxifraga hypnoides* (agg.) and *Arenaria verna*.

The slopes of the hills were largely calcareous pasture, that is, pasture without the heath plants.

WOODLAND ON THE CARBONIFEROUS LIMESTONE.

At the base of the Slieve Carran Cliffs a very fine thick hazel-scrub was met with. The bushes were fifteen to twenty feet in height, and, casting deep shade, sheltered a genuine woodland vegetation on the stiff marly soil with good mild humus. Associated with the hazel were Hawthorn, Ash, Holly, Mountain Ash, Birch, Wych Elm, *Euonymus europæus*, *Viburnum Opulus*, and *Rosa canina* (agg.) The hazel was, however, everywhere dominant, the other trees being present in small quantity. The woodland plants included *Oxalis acetosella* (sub-dominant), *Viola silvatica* (agg.), *Geum urbanum*, *Glechoma hederacea*, *Lysimachia nemorum*, *Scabiosa succisa*, *Angelica silvestris*, *Sanicula europæa*, *Circæa lutetiana*, *Veronica montana*, *Carex silvatica*, and *Epipactis latifolia* (agg.) The last named has usually been considered to be *E. atro-rubens*, but it was suggested that it was more probably *E. violacea*, or perhaps *E. media*. Finely developed mosses (*Hypnum* spp), *Polystichum angulare*, *Pteris aquilina*, *Ophioglossum vulgatum* were also present. Several other limestone valleys in the neighbourhood support considerable areas of hazel scrub, but these were not examined.

Garryland Wood (near Gort) was examined in some detail. At first there was some suspicion that it was mainly a planted wood, but on further examination it appeared that in parts at least it was a semi-natural wood. Parts of the wood were bordered by limestone pavement, with *Juniperus nana*, *Rosa spinosissima*, *Prunus spinosa*, etc. On the edge of the wood were hazel, holly, and yew, with *Rosa spinosissima*, *R. arvensis*, *Geranium sanguineum*, *Fragaria vesca*, *Spiræa Filipendula*, *Melampyrum pratense*, *Brachypodium silvaticum*, with a little *Calluna* and *Galium verum*.

¹ C. E. Moss. *Vegetation of the Bath and Bridgewater District*, Royal Geogr. Soc., 1906.

The wood itself contained *Quercus pedunculata* and *Fraxinus excelsior* (co-dominant in places and largely self-sown), *Ulmus montana* (self-sown, locally dominant), *Prunus spinosa* (abundant), *Pyrus malus*, *Cratægus monogyna*, *Corylus Avellana*, *Ilex aquifolium* (self-sown), *Viburnum Opulus*, *Euonymus europæus*, *Fagus silvatica* in places, *Rubus fruticosus* (agg.), *R. cæsius*, *Hedera Helix* (very abundant), *Lonicera periclymenum*, *Geum urbanum*, *Viola silvatica* (agg.), *Circæa lutetiana*, *Oxalis acetosella*, *Primula acaulis*, *Carex silvatica*, *Vicia sepium*, *Stellaria Holostea*, *Arum maculatum*, *Geranium Robertianum*, *Glechoma hederacea*, *Brachypodium silvaticum*, *Bromus asper*, the species of *Epipactis* met with in the hazel-scrub below Slieve Carran, *Aspidium Filix-mas*, *Polystichum angulare*, *Polypodium vulgare*. *Pteris aquilina* occurred, but was very scarce. In parts of the wood the oak was dominant and the ash scarce.

Although developed over limestone the soil over considerable tracts gave no calcareous reaction, and the general characters of the wood inclined to the oak- rather than to the ash-type. It is, however, quite possible that it has been derived from a wood of the ash-type by continuous accumulation of soil and washing out of lime, and this view is supported by the abundance of ash in parts, and the occurrence of species like the Spindle-tree and the Helleborine, as well as by analogy with various English woods.

BOTANY AT CHICAGO UNIVERSITY:

SOME IMPRESSIONS.

TO dream that one dwells in marble halls becomes a reality on entering Chicago University, which provides each of the great branches of learning with a spacious and handsome building on the "campus" or great stretch of wooded land it has acquired on the south side of the city. Overlooking the English Quadrangle and in sight of the Mitchell Tower, supposed to be to the Chicagoan what Magdalen Tower is to the Oxonian, stands the glass-crowned building devoted to the Botanical Department—admittedly one of the strongest in the Science Faculty.

With its two lecture rooms, five large private rooms for professors, seven or eight laboratories, a photographic room, and twelve private research rooms, it may well be the envy of the cramped London student, working in a building not many times larger, yet accommodating a dozen or more departments. Within, the genial professors, who are professorial in nothing but their scholarship, the assistants, and the students, from the gay young freshman to the newly made doctor, form one happy family, in which everyone knows, likes, and is not in the least in awe of anyone else.

You may sit on the stairs and discuss alternation of generations, or anything else with a professor, but you must jump up if anyone wants to pass, and not look as if it were inconsiderate for him to choose that particular moment, for the general atmosphere is that

expressed by the moral little mottoes seen tucked into the name-plate of a research room door, or framed on an office wall, "Keep Smiling," and "Don't Worry."

As may be imagined, the laboratories are splendidly equipped with every modern appliance, and the usual large scale of American work finds expression here in the hundred or more objects embedded at a time for the microtomes (of course running by electricity!), which cut ribbons often more than an inch wide, and daily afford a "potential output" of slides that only Professor Bower could estimate. The fossil slides bearing the familiar names of "Lomax" and "Dulesgate" are old friends to the English visitor, but they will soon have companions of American manufacture, for in the basement of the building is a fine machine for cutting rock sections and a mass of "Cycadella" material only awaiting the enthusiast with the necessary time and strength.

A most agreeable feature in the life of the Department is the weekly club meeting, open to all botanists, and preceded by tea, served with lemon instead of milk, and iced when the shade-temperature is above 90° F. Papers on original work done in the Department are read and briefly discussed, or critical accounts of recently published works are given by members of the Staff. During the fourth or summer quarter—peculiar to the University of Chicago, and throughout distinguished by special features—most interesting *resumés* are given, by specialists in the various subjects, on the present position and problems of morphology, physiology, ecology, laboratory technique, and the teaching of botany.

The elementary work of the Department is, perhaps, its least satisfactory side. Beginners have few, if any lectures. They read up a subject in a text-book, and, for practical work, study stained microtome preparations made for them by the demonstrators. They seem to examine very little material for themselves, and are quite incapable of cutting freehand sections, indeed I doubt if many of them realise such a possibility! I once astonished an advanced student with a preparation made in two minutes by the aid of a sharp razor and a simple water stain, from material fresh from the field, and one cannot help feeling that almost sole reliance on elaborate technique is a mistake, particularly in the training of embryo teachers, a numerous class of students, who later on, in their schools, are not likely to possess, and in any case would not have time to use, the multifarious apparatus so lavishly provided for them by their *Alma Mater*.

Botany, too, shares the disadvantage of all other undergraduate courses, which results from the large number of subjects required for the bachelor's degree, and the consequent impossibility of obtaining a thorough knowledge of any single one. This was curiously illustrated by a student, who had taken an advanced course of laboratory technique, but did not seem to possess rudimentary notions of floral morphology, though she was just about to graduate. Anxious British undergraduates, wondering if they will "get through," may envy the ease with which the Chicago student automatically takes his degree after three or four years of satisfactory work, untroubled by either "Intermediate" or "Final" examinations, but they may be consoled with the reflection that the bachelors are thought little more of than what indeed they are—

well educated school boys and school girls. (Our honour schools have no counterpart, at Chicago, and are scarcely understood). Even the externals of graduation as understood in this country are denied, for no mere bachelor (nor master either) is graced with a hood; that dignity is bestowed only with the highest degree conferred by the University, the Ph.D. The doctorate of philosophy may be taken in any branch of study, from theology to domestic economy, and requires a minimum of three years' study and the production of an original thesis. There is something about the higher degrees a little "through the looking glass" to English eyes, in the fact that names of candidates are published *before* the examination, and, with a remarkable sense of justice, the fee is only paid if the candidate is successful! The doctorate is granted in four grades, of which the highest, "summa cum laude," has never been given in the Botanical Department, but, so goes the legend, is being reserved for a second Darwin.

Lectures (always exactly to time) are of a very synthetic and informative character, and the points on which stress is laid are curiously complementary to those emphasised in this country. Relatively little is said of anatomy, and fossils naturally receive very sketchy treatment, but the facts of morphology, embryology, and physiology are dealt with in great detail, some lecturers encouraging intelligent questions, which certainly tend to elucidate matters. Nomenclature and classification are treated as regrettable necessities. Recent work, especially any done in the Department, is always to the front, and the general atmosphere in which all work is done is permeated by the spirit of investigation.

Nor can one praise too highly the treatment of research students. They are never hurried or interfered with, yet on the other hand are not neglected or left to feel that, graduation over, they can shift for themselves. The work in this direction is as carefully organized as in any other; some professors give a stated time in the week, when their research students can come and discuss the particular points reached, and receive encouragement and direction, while though originality is in every way given free play, a lecturer is always at hand to suggest a stain, discuss a theoretical point, or put in order a refractory microtome.

An inestimable help to the advanced student is the magnificent biological library, which seems to contain every book and publication one needs, including works in at least five different languages, and is presided over by a charming lady librarian, who knows where every book is or ought to be, and takes a pride in finding exactly what one wants in the shortest possible time.

Finally, one cannot close any account, however meagre, of this progressive and up-to-date corner of the botanical world "beneath the hope-filled western skies" without a tribute to the high character, geniality, and capacity for organization of him who inspires the confidence and loyalty of every member of the Department—the Director, John Merle Coulter.

T. L. P.

